From: kyle [mailto:kylew@eyesinthewoods.org]
Sent: Fri 1/8/2010 1:26 PM
To: Anderson, Philip M (DFW)
Cc: Commission (DFW)
Subject: EITW wolf plan letter

Date: 1/8/10

To: WDFW Director Phillip Anderson

CC: WDFW Commissioners

From: Kyle A. Winton (President)
Eyes In The Woods Association Inc. (EITW)

RE: EITW Board Concerns on the WDFW Wolf Conservation & Management Plan Options

Dear WDFW Director Anderson,

The Eyes In The Woods Association's mission is "to assist the appropriate State or Province agency or agencies, which governs their fish, wildlife, and natural resources (i.e., AFW, etc.), with the coordination of volunteer efforts, and to cooperate with other organizations in the policy of conservation, protection, and the perpetuation of our natural resources".

EITW is an assembly of certified and trained volunteers (mostly hunter/conservationists), assisting the WDFW for over a decade with enforcement education and wildlife science studies. The majority of our core volunteers have dedicated years of effort in Region-6 with Jack Smith on the "Roosevelt Elk Mortality Study", Roosevelt elk translocations, population/range and forage studies, Black Tailed deer studies, the collection of Chronic

Wasting Disease and DNA samples and hunter statistics; thus creating our vested conservation interest in ungallant populations.

Shortly after the 2009 Hunting Regulations were released; we received multiple communications from dedicated volunteers voicing concern that WDFW Wildlife Management is not following the mandated mission to attempt to maximize hunting opportunity and is ignoring the hunting population. The concern and complaints have increased greatly as more of the hunting/volunteer population has become aware of the proposed Wolf Plan options and the impact these will have on the ungallant populations of our state.

In November we were notified that non-profit funding promised to our Property Watch program to purchase an additional "Remote Camera System" for Eastern WA WDFW Access sites was not to materialize; as the organizations slated to contribute this funding are not going to support WDFW Wildlife management nor it's programs any longer due to the wolf plan process. Several EITW directors began research into their rational and our member's complaints; determining this to be a board priority and requesting it to be on the agenda.

Lee Davis (President, Kittitas Field and Stream Club & EITW Region-3 Training Coordinator) was invited to give us a briefing at our January 3rd Board of Directors (B.O.D) meeting; as he has conducted months of research on the Wolf Plan options, the process Wildlife Management used to develop these options and the science not included in the forming of the options. This includes examples of other states current issues and the up to date science including Scott Creel's study.

EITW directors investigated the current WDFW Wolf Plan options, the other states models and issues. After Mr. Davis's briefing on this subject; a lengthy discussion led the EITW-B.O.D to the decision that we are here to assist you and that we are obligated to voice our concerns as we feel the Agency is not understanding it's constituency. The B.O.D determined that we must inform you of the probable volunteer & financial repercussions the current options will have on the Agency.
First we are concerned that the hunting population is disenfranchised with the Agency and that hunter trust in the Agency appears to be at an all time low; adoption of any of these options as presented will increase this situation exponentially. As hunter demographics comprise the majority of EITW volunteers assisting the WDFW, retention of existing and the recruitment of future volunteers is at risk; directly impacting our ability to assist the WDFW.

It is our belief that the Agency will incur further loss of hunter trust; as a steady reduction of hunting activities will be required due to the estimated wolf population impact on ungallant populations and the length of time that will occur prior to any possible delisting.

A reduction of ungallant hunting activities will directly impact hunter generated funding (i.e. license/tag sales, Pitman Robertson funds, foundation funding, etc.) to the Agency. This is a great concern in this time of budget crisis. Impacts will also include the Aquatic Lands Enhancement Account funding that is vital to EITW projects and programs that assist the WDFW.

We question the following: Where is the dedicated funding for enforcement to deal with the additional dangerous wildlife? Where is the funding for damage to livestock? Where is the funding coming from to conduct the numerous studies on the breeding pairs of wolves? Where is the funding for the extensive studies necessary of the wolf impacts on ungallant populations? These are unanswered in the current plans and must be addressed to gain hunter support for any wolf plan.

It is the consumptive conservationist (the hunter), that began and continue the conservation movement. The same conservation mindset initially included establishing hunting regulations and the forming and funding of agencies that manage our wildlife; with the expressed purpose of ensuring that wildlife and the hunting heritage

continues in our state and nation. It is the same idealism that comprises the majority of EITW members; your volunteers.

As conservationists, EITW recognizes that wolves are here now, and will become a larger part of the predator base; yet caution must be used as this very efficient predator can damage years of ungallant conservation efforts and dollars spent. We are dedicated in assisting the WDFW and commission in achieving its Mandate (RCW 77.04.012 "The department shall preserve, protect, and manage the wildlife..., the commission shall attempt to maximize the public recreational game fishing and hunting opportunities for all citizens…"), and the goals of managing sustainable, diverse and healthy wildlife populations. We are concerned that the current options have not been well thought-out and will neuter the Agencies ability to achieve either.

It is the EITW Board of Directors hope that the Agency slows this process down and revisits the current options. Take the time to incorporate the additional science that's available and the other western states current wolf situations (not utilized in forming these options), thus forming a new set of options. It is critical that the hunting/conservationist community is engaged in the process as it is our funding that created wildlife management and the conservation movement. This may begin the process of reconnecting the Agency with the hunter, the conservationist, the volunteer; as they are all one and the same.

Sincerely,

Kyle A. Winton (EITW President)
360-870-0534

✓

RECEIVED
JAN 05 2010
HABITAT PROGRAM

January 4, 2010

Washington Department of Fish and Wildlife
State Environmental Policy Act Desk
600 Capitol Way North
Olympia, WA 98501-1091

RE: Comments on the WDFW Draft EIS for the Wolf Conservation and Management Plan

To Whom It May Concern:

The mission of the Upper Snoqualmie Valley Elk Management Group is to work collaboratively to minimize property damage and public safety risks associated with elk and to manage elk for a variety of recreational, educational and aesthetic purposes including hunting, scientific study, cultural and ceremonial uses by Native Americans, wildlife viewing and photography. Safety held first and problem animals removed.

Our group of stakeholders met in November and agreed to produce a statement which reflects our concerns as an elk management group. It is a stated objective of the draft plan to "address strategies to reduce conflicts." Reviewing the draft plan, our stakeholders have identified these primary concerns which should be clarified in the final plan:

1. Foremost, we are concerned that safety must be held first and problem wolves removed.

2. We are concerned that wolves may cause ungulates to congregate in settled areas more than now. This would increase management challenges.

3. We have public safety concerns about wolves being attracted to dense elk population in close proximity to settled areas.

4. We are concerned that our efforts to disperse the elk population by improving habitat in unsettled areas might be compromised by wolves moving into these same places.

5. Our group needs to work with the Department of Fish and Wildlife to coordinate our planning with the department's implementation of the Wolf Conservation and Management Plan. We request that the timelines for implementation of the plan in our study area and adjacent territories be communicated with sufficient advance notice to afford proactive planning.

Thank you for your consideration.

Sincerely,

David L. Willson

David Willson
President

Upper Snoqualmie Elk Management Group
Post Office Box 700
North Bend, WA 98045

3

12/14/09

To: WDFW
WDFW SEPA Desk
600 Capital Way N.
Olympia , Wa. 98501-1091

RECEIVED
DEC 21 2009
HABITAT PROGRAM

From: Oroville Sportsmens Club
POBox 2382
Oroville, Wa. 98844-2382
1-509-669-6088

Subject: Comments to Washington Draft Wolf Management Plan

Oroville Sportsmens Club is STRONGLY and unanimously OPPOSED to the RE-INTRODUCTION of WOLVES in Washington State for the following reasons -

1. The habitat and food abundance is not the same as when Wolves were present in large numbers in Washington state. We cannot turn back the clock to make it feasible for Wolves unless the state wants to eradicate other wildlife species.

2. A pack of Wolves is the most efficient preditor in North America and it is a deadly killer ; it has to be to live. All Game and Farm animals are potential Wolf food all year long.

3. In Okanogan county and most of Eastern Washington Deer wintering grounds are in or near valleys which are also occupied by ranches wintering Cattle, houses with Families and Orchards. Wolves must follow the food source and will without a doubt cause the same typeof problems for us that plague Idaho which has twice the wilderness area as Washington. In other states decimation of wildlife herds and depredation of Farm animals and Pets are occurring at high rates.

4. The Elk, Moose and Caribou population is just beginning to succeed and the Deer population is declining. Introduction of Wolves will eradicate them. WDFW will be sacrificing several species of wildlife for just Wolves. Other prediators will not survive unless they turn more to domestic Livestock and family Pets.

5. Once Wolves are introduced and their population has gone out of control, has WDFW planned ahead to deal with litigation expenses from people(ie) resisting any attempt to control Wolves by hunting or trapping, million dollar studies, federal laws, and lawsuits to prevent Wolf management ?

6. How can the state pay back losses of Cattle and other Farm animals due to the Wolves if the State of Washington has billions in deficit and is reducing WDFW's staff and

programs.

7. When all Game animal population in Eastern Washington are decimated will the State move to curtail hunting which will reduce revenues from hunting licenses and tourism? More tax revenues will then be lost for the State .

8. Most Ranchers and Orchardists have tried to mitigate Deer losses working with WDFW, will all of this hard work and expense be wasted if the Deer population is eradicated by a new species being introduced ?

In conclusion DO NOT introduce Wolves in Eastern Washington, both for the Wildlife and Washington State finances ; We CANNOT AFFORD the WOLVES !!!!

Mike Daharsh, President
Oroville Sportsmens Club
December 13,2009

Washington State Trappers Association
PO Box 3687
Arlington, WA 98223

RECEIVED
JAN 06 2010
HABITAT PROGRAM

January 4th 2010

WDFW SEPA Desk
600 Capitol Way North
Olympia, WA 98501-1091

Dear SEPA Desk:

After much study of The Washington State Department of Fish and Wildlife (WDFW) Draft Environmental Impact Statement (DEIS) alternatives regarding the repopulation of wolves into Washington, we find them all to be unacceptable, including WDFWs preferred alternative 2

Little argument can be made for not allowing wolves to naturally repopulate their former range. But, with seven of eight elk herds in the state below their targeted populations, we should not be trying to maximize predation. Alternatives 1, 2, and 3 do this by setting the number of breeding pairs too high for downgrading to threatened status, sensitive status, and final delisting. We support the repopulation of wolves in Washington, but at minimal levels. To do otherwise, with an already less than robust elk population, is inviting disaster. The wolf population should not be allowed to decimate our ungulate populations, but should be kept at a level where an optimum elk population can be maintained.

We also find the time frame to progress through the stages toward delisting to be unnacceptable. Status change should be triggered when the population reaches the targeted number, not after an arbitrary three year break.

We find the degradation of property rights to be appalling. People should be able to protect their property, and this includes pets and service animals as well as livestock, through all phases of the delisting process. The draft plan could result in an attack on humans if a wolf is allowed to take pets or service animals in close proximity to people with no consequences.

When delisting does occur, the wolf population should be managed through hunting and trapping. Licensed hunters and trappers should have the opportunity to harvest a wolf when they reach sustaining healthy populations after delisting.

The Cattlemen's Association has proposed a sensible alternative in Alt. 1A. The Washington State Trappers Association supports their well thought out approach. We would hope that the Fish and Wildlife Commission would adopt it.

Sincerely,
Bruce Vandervort
President, Washington State Trappers Association

✓ 9 2

From: Ron Bruno
To: SEPADesk2 (DFW);
cc: Commission (DFW); Director (DFW);
Linda Evans Parlette;
Subject: Wolf Conservation and Management Plan Public Comment
Date: Sunday, November 22, 2009 5:10:46 PM
Attachments: Wolf ltr 11-09.pdf

Please see the attached letter from the Wenatchee Sportsmen's Association as a public comment regarding the Wolf Conservation and Management Plan.

If you have any questions, please contact me on my cell phone number listed below.

Ron Bruno
President
Wenatchee Sportsmen's Association

Phone: 509-884-9369
Cell: 509-679-2359

Wenatchee
Sportsmen's Association

POST OFFICE BOX 762
WENATCHEE, WASHINGTON 98807-0762

November 20, 2009

Ms. Harriet Allen
Endangered and Threatened Species Section Manager
Washington Department of Fish and Wildlife
600 Capitol Way N
Olympia, WA 98501-1091

Dear Ms. Allen:

I am writing this letter to give a statement showing that the Wenatchee Sportsmen's Association is in full agreement with the minority opinion of the wolf working group – see attached letter.

We concur with these findings, and want to stress the point of the ever decreasing loss of habitat for all wildlife. The loss of habitat is causing the wildlife to group together, which makes for easy prey for the predators.

DNR's position of trading/leasing public lands for other land, which may not be as conducive for wildlife, is causing loss of habitat in critical areas due to either agriculture or structural development, which in some cases causes channeling of migration corridors.

When looking at the Washington state population density (people), and the lack of wildlife habitat, the number of wolves should be kept to a minimum to control future problems. Special emphasis should be given to winter wildlife feeding areas to keep wolves from potential mass killings of the wildlife.

We feel the better choice is to minimize problems for the wildlife, not to mention the financial complications, and ask you to consider and elect the minority opinion option, as it best directs issues concerned to the majority of sportsmen and allows co-habitation with wolves and other wildlife.

Sincerely,

Ron Bruno
President

Cc: Senator Linda Parlette
Phil Anderson, Director of Department of Wildlife
Wildlife Commissioners

May 27, 2008

Ms. Harriet Allen
Endangered and Threatened Species Section Manager
Washington Dept. Fish and Wildlife
600 Capitol Way N
Olympia, WA 98501-1091

The following represents a minority position held by the following members of the Wolf Working Group (WWG) Jack Field, Duane Cocking, Tommie Petrie, Daryl Asmussen, Jeff Dawson and Ken Oliver (We) on one critical component of the Wolf Working Group Plan; the number of Breeding Pairs (BP) of wolves that the state can support. We are "unable to live with" the proposed numbers in the WWG Draft Plan. We believe the numbers are too high and will result in direct conflict with the Livestock and Sportsman Communities.

Currently the plan calls for 6 BP's to down list to Threatened, 12 BP's to down list to State Sensitive and at least 15 BP's for 3 years before they can be considered for limited hunting(P.41 WWG draft). During this time period wolf populations could increase 24% per year (Bangs, conversation). Plus at the end of the 3 year time period, there is a very definite probability of one or more lawsuits as is now occurring after the Federal delisting of wolves in the Northern Rocky Mountain (NRM) area. It is estimated that it will take a minimum of 18 months for these challenges to work their way through the court system.

This same scenario will probably occur in this state. Consequently we could be looking at as many as 28 to 35 BP's before control measures could be taken to control their growth. All of this in a state with Washington's Population of 6,490,000 people and a population density of 97.5 people/sq mi (WWG Draft Plan). This is 5 to 6 times the human population density of the 3 principle states in the NRM area, MT, ID, and WY. (WA, WY, ID, and MT state web sites). According to the Federal Register, Feb.8, 2007, Vol.72, number 26 this state has only 297 square miles of suitable wolf habitat in the eastern third of the state (p.6117 Federal Register). It should be noted that this same source shows the following amounts of suitable habitat in each of the states comprising the NRM are, MT. 40924 sq. mi., WY. 29808 sq. mi., ID. 31,586 sq. mi., OR. 2556 sq. mi. and, UT. 1635 sq. mi. This same report indicates that if the 3 major states (ID, MT, and WY) can support 10 BP's for 3 years that the species can be considered to be fully recovered and can be considered for delisting (p.6107 Federal Register). That criteria was met in 2002 (p.6111 Federal Register).

The amount of suitable wolf habitat in the remaining two thirds of the state as depicted in the "Application of habitat models to wolf recovery planning in WA" by Carroll indicates scattered habitat in small isolated areas of the Okanogan, larger amounts of marginal habitat both North and South of Mt. Rainier, and a large area of habitat in and around the Olympic National Park, an area that strongly opposed wolf reintroduction several years ago.

Therefore we feel that the WWG's desired number of BP's is unrealistic given the lack of suitable habitat and the much higher human population density of this state and that the requirement of 15 BP's for 3 years (50% Higher that the USFW criteria for recovery in WY, MT, and ID,) defies common sense. This is further compounded by a recent recommendation from the Idaho Department of Fish and Game Commissioners to set the limit for a wolf hunt at 2005 levels which could mean 500 wolves could be killed this year. Idaho Fish and Game biologists estimate there are currently about 750 wolves in the state, but after the breeding season this spring they expect more than 1,000. The commissioners on the higher figures because they did not believe that hunting would bring the wolf population numbers down to the levels they wanted to see.

We therefore propose the following numbers of BP's statewide. 3 BP's to down list to Threatened, 6 BP's to down list to State Sensitive, and 8 BP's to change to a Big Game Animal. And we would eliminate the 3 year period since the state was not considered essential for recovery of wolves in the NRM (p.6119 Federal Register).
This total number of 8 BP's or approximately 80 wolves would fit in the states economic analysis as outlined in Chapter XIII, "Economics" which states "Wolf numbers between 50 and 100 animals should pose little detriment to the states livestock industry as a whole…As wolf populations become larger and more widely distributed, financial impacts are likely to accrue to more producers" (p.23 WWG Draft). "Populations of 50 to 100 wolves should not have negative effects on big game hunting in Washington," (p.38 WWG Draft).

The advantages of going with a lower number of BP's are: The sooner wolves can be removed from endangered and threatened status, the more tools stockmen and rural residents will have at their disposal to deal with problem wolves.

The sooner we can get wolves de-listed, the sooner our Fish and Wildlife Department can begin to manage them, until then their hands are tied. The sooner we can get them listed as a Big Game Species, the sooner our Fish and Wildlife can turn them from a liability into an asset through the sale of raffle tags, permits, and Governors Tags.

We believe that these numbers are far too high and do not accurately represent the concerns that the livestock production community has with wolves. The livestock community has preferred zero wolves from the beginning however, due to ESA and WDFW requirements zero is not an option. We support the Minority Opinion Numbers of 3 breeding pairs to downlist to threatened, 6 breeding pairs to downlist to sensitive, and 8 breeding pairs to delist from sensitive and managed as a Big Game Species. The higher numbers that the WWG Draft Plan includes will result in far more individual wolves than Washington has habitat to support thus causing a severe negative impact on private land owners and livestock producers. Livestock producers must be able to protect their property regardless of the wolf's status. We are also concerned that the WDFW has not effectively demonstrated its ability to secure long term funds that will be a requirement in Management and Compensation. Without funding there is **NO Support** of any plan!!

The remainder of the WWG plan is acceptable to the supporters of the minority position.

Jack Field Duane Cocking
Ken Oliver

Jack Field Duane Cocking Ken Oliver

Daryl Asmussen Jeff Dawson
Tommie Petrie

Daryl Asmussen Jeff Dawson Tommie Petrie

From: Seidman, Anna
To: SEPADesk2 (DFW);
Subject: Safari Club International and Safari Club International Foundation Comments on Washington Wolf Conservation and Management Plan
Date: Friday, January 08, 2010 2:00:29 PM
Attachments: Safari Club International Comments on Washington State Wolf Management Plan 1-08-2010.pdf

Dear Sir or Madam:

Attached please find Safari Club International and Safari Club International Foundation's comments on Washington's Draft Wolf Conservation and Management Plan.

If you have any questions about the attached comments, please feel free to contact me.

Thank you.

Anna M. Seidman
Director of Litigation
Safari Club International
501 2nd Street NE
Washington, D.C. 20002
202-543-8733
aseidman@safariclub.org

"Nothing in the world can take the place of persistence. Talent will not; nothing is more common than unsuccessful men with talent. Genius will not; unrewarded genius is almost a proverb. Education will not; the world is full of educated derelicts. Persistence and determination alone are omnipotent. The slogan 'Press On' has solved and always will solve the problems of the human race."

Calvin Coolidge

This transmittal may be a confidential attorney-client communication or may otherwise be privileged or confidential. If you are not the intended recipient, you are hereby notified that you have received this transmittal in error. Any review, dissemination, distribution or copying of the contents of this e-mail is strictly prohibited. If you have received this e-mail in error, please notify us immediately.

Washington Department of Fish and Wildlife
SEPAdesk2@dfw.wa.gov

Dear Sir or Madam:

Safari Club International and Safari Club International Foundation (SCI and SCIF) appreciate the opportunity to comment on the Draft Wolf Conservation and Management Plan for Washington (Draft Plan).

SCI and SCIF support the State of Washington's attempt to devise a conservation and management scheme for its wolf population. We also support Washington's decision to establish target breeding pair numbers to trigger listing decisions and changes in management strategies. We do, however, have some concerns with the way that the Draft Plan generally and the preferred alternative specifically address the impact that wolves will have on game species and hunting opportunities in the state. In addition, the Draft Plan fails to address the question of how the state wildlife management authority will deal with the population of wolves once they exceed the delisting target threshold.

Safari Club International and Safari Club International Foundation

Safari Club International, a nonprofit IRC § 501(c)(4) corporation, has approximately 53,000 members worldwide, including many who live and/or hunt in Washington State. SCI has six chapters in Washington and these chapters are extremely active in the proper conservation and management of Washington's wildlife resources. SCI's missions, in Washington, and throughout the world, include the conservation of wildlife, protection of the hunter, and education of the public concerning hunting and its use as a conservation tool.

Safari Club International Foundation is a nonprofit IRC § 501(c)(3) corporation. Its missions include the conservation of wildlife, education of the public concerning hunting and its use as a conservation tool, and humanitarian services. More specifically, the conservation mission of SCIF is: (a) to support the conservation of the various species and populations of game animals and other wildlife and the habitats on which they depend; and (b) to demonstrate the importance of hunting as a conservation and management tool in the development, funding and operation of wildlife conservation programs.

SCI and SCIF have participated on multiple occasions in litigation in federal court concerning the delisting of the wolves of the Northern Rocky Mountains. We are currently participating as intervenors in the suit in U.S. District Court in Montana over the delisting of the Northern Rocky Mountain distinct population segment of wolves, which includes those in Washington. We have worked with and supported the delisting and management efforts of Montana and Idaho and are more than familiar with many of the struggles that the states have encountered in their attempt to regain management authority over their wolves. It is

our hope that Washington can learn a great deal from the experiences of the states whose management plans have already been and are currently being scrutinized by the federal courts. There is also much to learn from specific organizations, such as SCI and SCIF, and the hunting community generally who are on the front lines when it comes to co-existing with wolf populations and defending the management authority of the states as they deal with those wolf populations.

The Draft Plan Requires Enhanced Consideration of the Impact of Wolves on Hunting Opportunities

SCI and SCIF request that the drafters of the Draft Plan revisit the proposed strategy to deal with the impact that wolves will have on ungulate abundance and behavior. The Draft Plan offers a detailed discussion of the significance of hunting, and particularly the ungulate populations that are the subject of that hunting, to Washington. For example, the Draft Plan notes both the recreational and economic interests served by hunting. "[H]ealthy and abundant prey populations are important for maintaining hunting opportunities that contribute to many local economies in Washington, especially in more rural regions." Draft Plan at 56. The availability of healthy, sustainable large ungulate populations is of great significance to the almost 200,000 individuals who hunt in the state:

> An estimated 182,000 hunters hunted in Washington in 2006, with an estimated 179,000 residents and 3,000 non-residents participating. Hunters spent nearly 2.13 million days hunting for all species in the state in 2006. *Big game hunting represents some of the most highly valued hunting in Washington*, with an estimated 90% of hunters hunting ungulates in 2006 (USFWS and USCB 2008).

Id. (emphasis added). Despite the significance of large game hunting in the state, the preferred alternative expresses the state's plan to reduce hunting opportunities in the event that the growth of wolf populations has a detrimental impact on the wild ungulate species that are the focus of the state's hunters. Alternative 2 states:

> Alternative 2 would manage for healthy ungulate prey populations through standard practices, and would also allow for consideration of some adjustment of recreational harvest levels, if needed, to benefit wolf conservation in certain limited situations. Both scenarios could result in some management restrictions being placed on harvest levels (e.g., reductions in antlerless take, shortened hunting seasons, and reduced availability of special permits) in localized areas.

Draft Plan at 25. The Draft Plan passively makes recreational hunting, including the businesses and communities that currently depend on those ungulate populations for hunting, an accepted casualty of wolf conservation. Although the Draft Plan does

contemplate wolf reduction and/or relocation to respond to profound ungulate population declines, such strategies will not be implemented until the ungulate populations are found to be "at-risk" and only after hunting opportunities have significantly declined or have been mandatorily restricted. In other words, the Draft Plan allows wolf populations to grow and spread until they cause a problem to the ungulates, the hunting community, and ultimately the wolves that depend on the presence of healthy ungulate populations.

> Under this alternative, management of at-risk ungulate populations could consider removal of wolves under certain limited circumstances after delisting occurs. Although hunting of at-risk populations would likely already be prohibited or tightly restricted, removal of wolves could enhance future hunting opportunities.

Draft Plan at 58. The preferred alternative plans to follow a scenario that will first allow the problem to occur and only after there is a problem will the wildlife management authority take action to alleviate that situation. SCI and SCIF strongly recommend that the Draft Plan be revised to avoid problems, rather than to create and react to them.

The Draft Plan attempts to obscure this obvious flaw by suggesting that there is insufficient evidence to demonstrate that wolf predation is causing a decline in large ungulate populations. However, numerous references in the Draft Plan dispute that supposition. For example, although the Draft Plan disputes statewide ungulate declines, it admits the likelihood of "localized impacts on ungulate abundance or habitat use." Draft Plan at 8. The Draft Plan also acknowledges that wolves choose to prey on young ungulates. Those preyed-upon young ungulates are not making it to adulthood to help sustain population numbers. Draft Plan at 46. Similarly, the Draft Plan acknowledges evidence that elk, in responding to wolf presence, are spending less time feeding and are moving to safer habitats with poorer nutritional quality, and that the resultant lower calf production will have a detrimental impact on ungulate numbers. [Creel et al. (2009)] Draft Plan at 46.

The Draft Plan also suggests that where ungulate populations are in decline, wolves may only be one of multiple factors contributing to that decline. Whether wolves are the exclusive cause of elk and other ungulate species decline, or whether they are one of several factors contributing to declining herd numbers is irrelevant. If the fish and game agency has the power to control one or more factors that are harming the state's wildlife populations, then the agency should exercise that authority. And if ungulate populations are already suffering due to habitat decline, severe winter weather and increasing populations of other predators, it would be poor management practice for the fish and game agency to introduce another cause of decline, namely wolves, and then to fail to aggressively prevent that additional factor from further harming the game species. Draft Plan at 29.

Though a challenging task, the drafters of the Draft Plan should find better means of addressing the impact of wolves on ungulate population health, behavior and numbers and

on the hunting opportunities that depend on those ungulates. It is irresponsible to force the hunting community to bear the brunt of the impacts of wolf conservation and to allow the state's ungulate populations to reach an "at-risk" state before controlling or removing an acknowledged source of that risk. An approach that will work and garner the support of the hunting community must be pro-active and must conserve not just the wolves but the ungulates and the interests of hunting at the same time.

SCI and SCIF Recommend the Development of Targeted Maximums

The Draft Plan is open-ended. It declares breeding pair target numbers for reclassifying and delisting wolves, but stops there. The Draft Plan includes no maximum or target numbers for long-term sustainability. If Washington's wolf conservation efforts are successful, wolf numbers will increase and Washington will face the same problem currently being experienced by Montana, Idaho and Wyoming – namely how many wolves is too many. This issue is not adequately addressed by a delisting threshold of 15 breeding pair. Although delisting allows more aggressive management strategies, it does not address the question of the number of wolves that the state wishes to manage and maintain on a long term basis. There is a difference between the minimum number necessary for removing federal or state protections, and the number that can be managed in balance with the conservation of the state's wild game populations, domestic species, public perception and the health of the hunting industry. SCI and SCIF recommend that the state fish and game agency analyze this issue and confront this question before finalizing the plan.

Thank you for this opportunity to comment on Washington's efforts to manage its wolves. If you have any further questions, please contact Anna M. Seidman, Director of Litigation for Safari Club International at 202-543-8733 or aseidman@safariclub.org.

Sincerely,

Lawrence Rudolph
President,
Safari Club International
Safari Club International Foundation

28

From:	Jim Mullen
To:	SEPADesk2 (DFW);
cc:	Tom Perry; WWC_BoD@yahoogroups.com;
Subject:	Comments on the WDFW Draft EIS for the Wolf Conservation and Management Plan (Corrected Copy)
Date:	Thursday, January 07, 2010 10:14:20 PM

Ladies and Gentlemen

Washingtonians for Wildlife Conservation (WWC) and Hunters Heritage Council (HHC) would like to provide the following six items for entry into the public record as Comments on the WDFW EIS for the Wolf Conservation and Management Plan.

1. Well regulated hunting is essential for the sound and responsible management of wolves in Washington and for the safety of the general public and their animals.

2. The sale of hunting tags is a source of revenue that produces funding for conservation efforts.

3. Efforts are required to insure that wolf populations don't become so large that the animals become a menace and there is a public backlash against their presence as there is with cougars in some areas of the state.

4. Control efforts should include ways of engendering a desire for separation from the public and their animals. Hunting is one of the best ways to accomplish this.

5. Control efforts must be effective enough that the species upon which wolves prey do not become endangered or extinct.

6. Control efforts must be effective enough that domestic livestock losses do not become burdensome for the livestock industry.

Thank you for your consideration.

Jim Mullen
President, Washingtonians for Wildlife Conservation

Tom Perry
President, Hunters Heritage Council

Kittitas County Field & Stream Club, Inc.
P.O. Box 522
Ellensburg, WA 98926

"Working Today For Tomorrow's Wildlife"

RECEIVED
JAN 14 2010
HABITAT PROGRAM

31 Dec 2009

FROM: Kittitas County Field & Stream Club

SUBJECT: WDFW Wolf Conservation and Management Plan

TO: Governor Chris Gregoire
WDFW Director, Phil Anderson
WDFW Commissioners
Dave Britell, Wildlife Management
Dave Ware, Wildlife Management
Harriet Allen, Wildlife Diversity

CC: Sen. Janea Holmquist
Rep. Judy Warnick
Rep. Bill Hinkle

ATTACHMENTS:
WDFW Wolf Working Group Minority Letter

The Kittitas County Field & Stream Club is opposed to all alternatives of the current Wolf Conservation and Management Plan for Washington. Alternatives 1, 2 and 3 for wolf recovery and management are unacceptable and alternative 4 "no plan" is also unacceptable. Simply stated each alternative uses the same down listing and delisting numbers of breeding pairs. The proposed breeding pair numbers are excessive in relation to Washington States demographics, available fragmented habitat and its carrying capacity.

We propose the following numbers of BP's statewide. 3 BP's to down list to Threatened, 6 BP's to down list to State Sensitive, and 8 BP's to change to a Big Game Animal. Additionally we propose that when 4 breeding pairs are confirmed to exist that the WDFW Game Division form a committee to formulate the process and implementation of Wolves as a game species. This could be, or start as a function of the Game Management Advisory Committee. This process needs to be completed well before delisting as other states have found that this in itself is a lengthy process that needs to be well organized, researched and planned. The timing of this and other existing parts of the plan are critical as we prepare for the eventual delisting of the Gray Wolf.

Failure could jeopardize the population objectives of other species and/or result in increased costs to the state

GEOGRAPHY:

Washington is unique compared to other western states with existing Wolf Management Plans in place. Washington has a population density of 97.2 per square mile. That is 5 to 6 times that of the other western states. Our potential habitat is eleven to fifteen percent of other western states and even that is fragmented. Even our prey base wildlife has denser populations per square mile. Fragmentation, human encroachment, urbanization, highways and interstates best describe the boundaries of most of our public lands and wildlife areas.

Final EIS of 2009-2015 Game Management Plan states – *"Washington has the second largest human population of the western contiguous states, but is the smallest in size. In 2007, the population was estimated at 6,488,000 compared to 5,974,900 in 2001 making it the 13th most populous state in the union. The long-term outlook in human population for the state of Washington is continued growth, with ever increasing impacts to the natural resources of the state."*

POPULATION & PREDATOR-PREY INTERACTIONS:

At minimum assumptions - One "breeding pair" of wolves is assumed per pack, and a pack is considered by the U.S. Fish and Wildlife Service to contain 10 wolves. Thus 15 breeding pairs would put at least 150 gray wolves in the state—a level the DFW and the DEIS authors consider "minimal or barely adequate for achieving population viability and recovery." At the end of 2008 Montana had 497 wolves but only 34 of 84 packs qualified as breeding pairs. *Montana (2008) Gray Wolf Conservation and Management Reports - "A total of 84 verified packs of 2 or more wolves yielded a minimum estimate of 497 wolves in Montana. Thirty-four packs qualified as a Breeding Pair according to the federal recovery definition (an adult male and female with two surviving pups on December 31).* At a documented *(USFWS 2009)* average of 24 percent growth per year, we would have nearly 300 wolves in Washington before delisting could happen as a result of the stipulation inserted that 15 breeding pairs be maintained for three consecutive years. With that stated add the two years other states have typically dealt with lawsuits and injunctions, and we are looking at nearly 500 wolves before their numbers could be managed. *White et al. (2005)* estimated annual kill rates *"have been closer to 22 ungulates per wolf per year,"* based on an assumption that summer kill rates are approximately 70% of winter kill rates. Additional research is currently being conducted to document summer prey selection and kill rates. Based on these assumption wolves could consume 11,000 elk per year in the final year of litigation. Washington State's total elk population is only slightly more than 50,000 elk *(2009-2015 WDFW Game Mngmnt Plan)*. These numbers are not sustainable. Even at only 300 wolves those numbers are not sustainable. Simply stated the number of breeding pairs for delisting must be lower and remove the three consecutive year policy. An anonymous WDFW employee in the wildlife department agrees that this (15 breeding pairs and 3 consecutive year wait) scenario could potentially devastate the elk herds.

The impacts of wolves on prey abundance have been, and continue to be, widely debated. A number of studies indicate that wolf predation can limit ungulate prey populations. Population-level effects result primarily through predation on young-of-the-year and older weaker ungulates and are frequently enhanced when occurring in combination with other predators. There is also the indirect effect on Elk populations. Elk respond to the presence of wolves by spending less time feeding and moving to safer habitats of poorer nutritional quality, resulting in reduced nutrition and lowered calf production that pushes the population downward.

A recent study by University of Montana researchers released this year which appears in the "Proceedings of the National Academy of Science" disproves what many biologists and experts previously believed. This study is a perfect example of why we believe the DEIS and Wolf Management Plan need reviewed and adjusted. The references used and science referenced in the DEIS and Wolf Management Plan is outdated. NUMEROUS studies on Gray Wolf behavior have been completed and released recently. Until this new research conducted by S.Creel/Montana State University was released experts denied that Wolves were responsible for lower elk populations in some areas using direct predation studies as their basis. We all agree wolves kill elk, and direct predation is responsible for much of the decline in elk numbers in some areas, but the rate of direct killing was not great enough to account for the elk population declines observed. Weather, nutrition, disease and other influences were blamed.
Creel's study is attached and this is a summary of his work.

(S.Creel/MSU) *"Wolves have caused elk in the Greater Yellowstone Ecosystem to change their behavior and foraging habits so much so that herds are having fewer calves, mainly due to changes in their nutrition,*
During winter, nearly all elk in the Greater Yellowstone Ecosystem are losing weight. Essentially, they are slowly starving.
With the presence of wolves, elk browse more - eating woody shrubs or low tree branches in forested areas where they are safer.
Elk regularly hunted by wolves are essentially starving faster than those not hunted by wolves. In addition to direct predation, the decline is due to low calving rates, which are a subtle but important effect of the wolves' presence. We knew the presence of wolves caused lower calf-cow ratios, but we didn't know why. Radio collaring calves revealed that calf numbers were low immediately after the birth pulse, suggesting that a decline in the birth rate was part of the population decline.
This suggestion was confirmed when the researchers found that elk facing high levels of predation risk had substantially decreased progesterone levels prior to the annual birth pulse. Progesterone is necessary to maintain pregnancy, but a question remained: what was responsible for the decrease in progesterone?
There were two competing theories: One suggested elk suffered from chronic stress due to the wolves' presence. In all mammals, stress causes the release of cortisol, a hormone that helps free up energy to either fight or flee. But too much cortisol from chronic stress can cause the immune and reproductive systems to shut down.
The other theory was that the elk weren't getting enough to eat because they were always on the run from the wolves and spending more time in the forest, where food is sparse compared to

grassy meadows. For wintering elk that are already on the edge of starvation, anything compromising nutrition could also cause the reproductive system to shut down.
The elk are trading reproduction for longevity.
Elk are potentially long-lived, and many prior studies have shown that, in species like this, natural selection favors individuals who do not compromise their own survival for the sake of a single reproductive opportunity."
If predators commonly affect the reproduction of their prey, it will change the thinking about predator-prey dynamics, and might change how wildlife managers plan for the reintroduction of predators."
"This research shows that the total effect of a predator on prey numbers can be larger than one would determine simply by looking at the number that are killed."
"Until now, it would have seemed obvious to conclude that a herd losing many of its number to predators would decline faster than a herd where predators were less successful."

"However, now it is conceivable that the herd with the lower direct predation rate could decline faster, if it spends more of its time and energy avoiding being eaten and less on reproduction," S.Creel/MSU Lead Author of Glucocorticoid stress hormones and the effect of predation risk on elk reproduction.

Reasons exist why research varies from state to state and region to region about wolves' effects on ungulate populations. The dynamics of Wolf - prey populations has unique ecological conditions at each location and they are very complex. Researchers say the seemingly contradictory findings show that not all elk populations respond in the same ways when they share the land with wolves. *"One-size-fits-all explanations of wolf-elk interactions across large landscapes do not seem to exist,"* Justin Gude, MFWP's chief of wildlife research.

One very important piece of data that seems present in all conditions was whether prey populations existed at or below its carrying capacity during reintroduction of wolves. This was a noted and important element in assessing the results of several studies *(D. W. Smith, pers. comm.)* According to the *(Final EIS of the 2009 – 2015 Game Management Plan)* **6 out of the 10** Elk herds in Washington State are currently below the **MINIMUM** population objective range.

Montana wolf packs include a combination of public and private lands. The average pack territory in Montana is comprised of about 30% private land. Most Montana packs do not live strictly in back country wilderness areas or solely on public lands. Of the 84 packs in Montana, only 15 percent reside most of the year in the remote backcountry. Many others live in public land areas with more public access and habitat fragmentation than wilderness areas. However, the majority of Montana wolf packs live in areas where mountainous terrain, intermountain valleys, and public / private lands are intermixed. *(Montana Gray Wolf Conservation & Management annual report (2008).*

WDFW has eight permanent existing winter feeding sites and over 160 miles of fence line for Elk and Big Horn Sheep in Kittitas and Yakima counties alone. This is a result of a lack of connectivity between summer and winter range, no winter range and elk damage to commercial

agricultural crops, orchards, and vineyards which occurs primarily in the winter. Final EIS states *"A large percentage of what is considered historic elk winter range before European settlement has been removed due to agriculture and housing development. At current population levels, some elk in Washington must be fed every winter due to inadequate winter range. To prevent elk in the Yakima herd from causing agricultural damage, elk fencing and a winter feeding program was established. Elk winter-feeding programs can be problematic. They are expensive and cause elk to congregate at high densities,"* Only Wyoming of the other western states has the unique issue of regularly established winter feeding sites. In fact 22 feeding stations and three of those have undergone detailed scientific data collection. Wyoming has incurred increased costs in manpower, hay, fence repair and damage to surrounding habitats and agricultural lands. Elk dispersal from wolf presence at the feed sites has caused elk/vehicle collisions and/or conflicts on adjacent highways at 6 different feeding stations. The Washington Wolf Management Plan does not address these feeding site issues other than to simply state.
"These situations will be evaluated on a case-specific basis to determine if management responses are needed and, if so, what the responses should be". That is unacceptable. Predation will occur at feeding stations where there will be high concentrations of elk. It is already documented in Wyoming that wolves target the fringes of feeding sites and at times move in closer causing highly concentrated numbers of elk to quickly disperse. Calf recruitment rates are affected greatly in herds that depend on winter feeding sites as a result of depredation and/or increased presence alone. Even locally in Kittitas County WDFW feed crews have observed trophy bull elk clear 8 foot elk fences. Rare but it provides insight on the agile ability of elk to elude predators if needed. By having such high numbers of breeding pairs for down listing and delisting you have removed the ability of WDFW conflict specialists and game managers to handle this situation. I was informed by one of these managers that until delisting they would not have the appropriate tools or methods available to them to address it. (Public meeting Wenatchee, WA)

TRANSLOCATION:

Reintroduction of wolves to their historic range often fail (Kleiman 1989; Fischer and Lindenmayer2000) and translocated wolves typically have lower survival rates than non-translocated wolves and are less likely to establish or join a pack (Bradley and others 2005). Wolves in Washington should be allowed to move into and inhabit on their own. This natural inhabitation process will according to experts occur over a long period of time. Translocation according to the working group is only considered as an option to speed up the recovery effort so that delisting can occur. Only after delisting does WDFW have sufficient management tools available to address our unique situations in a highly populated environment. You can achieve the same result in giving wildlife managers flexibility by not placing such high down listing and delisting numbers of wolves in the plan. Lower wolf numbers will also ensure sustainable ungulate populations that are already in decline. Wildlife managers are struggling to keep them at sustainable levels already. The following is from the current 2009-2015 WDFW Game Management Plan."*Nearly all of the state's elk herds are being impacted by development and other built environments as a result of the human population increase. In some cases it involves housing developments, in other cases; it may be low density or recreational development."*

Again, the Final EIS of the 2009 – 2015 Game Management Plan states 6 out of the 10 Elk herds in Washington State are currently below the MINIMUM population objective range.

Remove translocation from the options for the South Cascades, Olympic Peninsula and remove the predetermined number of wolves and breeding pairs per region for delisting. As wolves migrate and packs develop use this information for a scientific basis to determine the carrying capacity of wolves for each region. We may find some regions can sustain more than we believed possible and other regions may have a reduced number. Any hunting options or harvest rates would still need to be addressed and approved by the WDFW Commission. If considered and approved harvest and management needs with consideration to population objectives can then be established as needed on a regional or a more localized level of Game Management Units on an annually adjusted basis. It should be recognized in the plan that hunters are a management tool. Wildlife managers have used hunters effectively in balancing various species with great success. In fact, no species has EVER gone extinct through managed hunting.

As much as we'd like to see some of history reversed it is not reasonable to even think wolves will return to the various reaches of our state without additional human intervention. It is the unneeded human intervention such as translocation that will cause the most strife for not only the citizens but the wolves as well. Your own DEIS, 3.A (Distribution) States. *" It is not possible at this time to predict the eventual distribution of wolves in Washington or the carrying capacity of landscape to support them."* They will move into and populate the areas they feel are conducive to their sustainable existence. Just as current science has proven they will not inter breed, and they will naturally split into other packs with new breeding pairs. The wolves will and must be allowed to be their own guides in their movement and genetic diversity.

CONTROL VS HUNTING:

Wyoming wildlife has taken some serious hits—especially in the western part of the state—as wolf numbers have grown well beyond the original target numbers (non-hunted wolf populations in the Northern Rockies increase between 20 and 26 percent annually). Wildlife killed by wolves has come from the same population which hunters use. Moose hunting permits have dropped precipitously in the last decade, paralleling the increasing scarcity of moose in western Wyoming. Outfitters and Game Department personnel have been posting observations of low numbers of calf elk running with elk herds by late summer. In response to all this, Wyoming Game and Fish developed regulations to manage wolves.

Their plan involved harvesting "non-essential" wolves, which are those outside the recovery zone. The plan was a widely-discussed attempt to satisfy the U.S. Fish and Wildlife Service's concerns about state management. A dozen conservation groups stood ready to file lawsuits should USF&WS give the state management. The bottom line is that Wyoming has lost its ability to manage its wolves—they now belong to the Feds—and wolf numbers just keep growing.

On the other hand, both Montana and Idaho had plans approved by the Feds. Both states set hunting seasons for this fall, and both seasons have withstood proposed injunctions and lawsuits.

Montana has a hunt underway, with a goal of taking 75 wolves, while Idaho's three-part season is to remove 220 animals. Both of these hunts are to help meet the states' population objectives under their approved management plans.

GAME ANIMAL AFTER DELISTING:

The DEIS does not mention nor does it follow the mandates that the Washington State Legislature set forth for the WDFW in (RCW 77.04.012)

> *"..the department shall preserve, protect, perpetuate, and manage the wildlife..."; and "The commission shall attempt to maximize the public recreation...hunting opportunities of all citizens, including juvenile disabled, and senior citizens..."*

Wolf populations have a high reproductive capacity and a great deal of demographic resilience and persistence (*Fuller et al 2003*). Wolf populations are highly resistant to humane taking. It has been well demonstrated that wolf populations can sustain annual harvest rates of up to 50% of their populations per year (*Fuller et al.2003*). This is supported by David Mech PhD. one of the world's foremost wolf authority's, in his declaration to the U.S. District Court for the District of Montana (Missoula, Montana) on 09/25/09.

The WDFW's DEIS & its four alternatives are remiss by not mentioning the use of hunters as a tool for wolf control after delisting and giving the wolf game status. After delisting the Wolf needs to be managed as a Game Animal and hunters should be utilized as a tool for control as needed.

Ungulate populations are important to not only wolves and other carnivores, but to sportsmen, licensed guides and others in the State whose income depends upon hunting and other wildlife-related activities. Hunting licenses fund the majority of wildlife management and conservation in Washington. It is important that the State balance the wolves' need for prey with the public's investment in these ungulate populations in order to maintain the public's opportunity to hunt and otherwise enjoy them in a sustainable and responsible manner.

Joe Maurier, Director Montana Fish, Wildlife & Parks recently wrote the following in his article titled " In Our Opinion" in the November 2009 issue of "Montana Outdoors".

"Montana's wolf hunting season will not endanger the health of the wolf population. State and federal monitoring shows that wolves continue to move among subpopulations in the three recovery zones—the Greater Yellowstone Ecosystem, northwestern Montana, and central Idaho—as well as to and from Canada. This movement will help maintain genetic diversity. Montana's wolf season was designed to not impede wolf dispersal, such as by stipulating that no more than 25 percent of the harvest can come during December, when wolves are especially mobile and moving among subpopulations. While Montana's wolf population will remain healthy, it still needs control to retain a reasonable balance of the carnivores and other wildlife. In hunting districts near Yellowstone, wolves have killed up to 20 percent of the elk. Calf recruitment in parts of the Bitterroots this past spring dropped to a record low. And wolves may be worsening the effects of recent severe winters on northwestern whitetail populations. Also, 77 cattle and 111 sheep were confirmed as killed by wolves last year, and more wolf depredations

likely occurred but could not be verified. The wolf hunting season is intended to help reduce livestock losses and lessen effects on wild ungulate populations."

WILDLIFE TOURISM:

In the DEIS under section D, Wildlife Tourism is quoted as *"Ecotourism, or travel to natural areas for environmentally responsible outdoor experiences, is one of the fastest growing segments of the overall world tourism industry. Wildlife viewing is a large part of this business and is hugely popular in the United States." "In Washington during 2006, an estimated 2.33 million people 16 years old and older participated in some form of wildlife watching, which ranked the state 11th in the nation for participation (USFWS3 and USCB 2007, 2008)" "Annual spending in Washington by resident and non-resident wildlife watchers on travel, food, lodging, equipment, and other goods and services totaled an estimated $1.5 billion in 2006, ranking the state seventh in the nation behind California, Florida, Texas, Michigan, Georgia, and New York (USFWS and USCB 2007, 2008).* This paints a rosy picture leading one to believe wolves may be an integral part of wildlife tourism. The following is listed in the very last line of this section which is key to the plan. *"However, revenue to WDFW for wildlife conservation and management generated by wildlife watchers is minimal."* The DEIS conveniently left out one KEY PART of recent surveys which is ***"Wildlife viewing is often a secondary activity associated with primary trip such as hiking or camping."*** It also fails to mention that of the 2.33 million residents that watched wildlife **sixty-seven per-cent** did so within 1 mile of their residence or at their residence. The 2.33 million wildlife watcher number also includes the couple hundred thousand resident sportsmen that also watch wildlife. So, the true numbers of wildlife watchers that are not licensed sportsmen and that travel for the primary purpose of watching wildlife are much lower. The DEIS is very misleading on this issue. Let us remind you again that in reality the sale of hunting licenses, tags, and stamps is the primary source of funding for WDFW and state wildlife conservation efforts. By purchasing licenses, and paying federal excise taxes on hunting equipment and ammunition, individual hunters make the largest contribution towards ensuring the future of many species of wildlife and habitat. By paying the Federal excise tax on hunting equipment, Washington State hunters are contributing millions of dollars for conservation programs that benefit many wildlife species, hunted and non- hunted.

SUMMARY:

Washington public lands and wildlife are already in a very fragile balance. We support wolves in Washington and agree they will create a different and interesting aspect to the balance of wildlife. There will be adjustments hunters will have to make for successful hunts as big game will have another predator in the mix. There will be at times minor adjustments in hunting harvest in big game as there is now based on population objectives that can be low at times that occur from disease and harsh winters. Cattle, sheep and pet depredation can and will occur. As sportsmen, recreationists and citizens we insist that the working group and/or WDFW adjust this current plan to be more flexible in numbers, pairs and locations of wolves based on THEIR ability to adapt

The Kittitas County Field & Stream Club believes the down listing and delisting numbers of 3, 6 & 8 should be supported without constraints on regions. Not the proposed numbers of 6, 12 and 15. The wolf populations should be managed on carrying capacity, social tolerance, for hunter harvest and not simply on prey abundance. The latter of which goes against the RCW mandate for WDFW but also the 2009 -2015 Game Management Plan. Additionally we support the statement of the members of the working group who submitted the attached minority report submitted on May 27, 2008.

Kittitas County Field & Stream Club Inc.

Lee Davis, President

May 27, 2008

RECEIVED
JAN 14 2010
HABITAT PROGRAM

Ms. Harriet Allen
Endangered and Threatened Species Section Manager
Washington Dept. Fish and Wildlife
600 Capitol Way N
Olympia, WA 98501-1091

The following represents a minority position held by the following members of the Wolf Working Group (WWG) Jack Field, Duane Cocking, Tommie Petrie, Daryl Asmussen, Jeff Dawson and Ken Oliver (We) on one critical component of the Wolf Working Group Plan; the number of Breeding Pairs (BP) of wolves that the state can support. We are "unable to live with" the proposed numbers in the WWG Draft Plan. We believe the numbers are too high and will result in direct conflict with the Livestock and Sportsman Communities.

Currently the plan calls for 6 BP's to down list to Threatened, 12 BP's to down list to State Sensitive and at least 15 BP's for 3 years before they can be considered for limited hunting(P.41 WWG draft). During this time period wolf populations could increase 24% per year (Bangs, conversation). Plus at the end of the 3 year time period, there is a very definite probability of one or more lawsuits as is now occurring after the Federal delisting of wolves in the Northern Rocky Mountain (NRM) area. It is estimated that it will take a minimum of 18 months for these challenges to work their way through the court system.

This same scenario will probably occur in this state. Consequently we could be looking at as many as 28 to 35 BP's before control measures could be taken to control their growth. All of this in a state with Washington's Population of 6,490,000 people and a population density of 97.5 people/sq mi (WWG Draft Plan). This is 5 to 6 times the human population density of the 3 principle states in the NRM area, MT, ID, and WY. (WA, WY, ID, and MT state web sites). According to the Federal Register, Feb.8, 2007, Vol.72, number 26 this state has only 297 square miles of suitable wolf habitat in the eastern third of the state (p.6117 Federal Register). It should be noted that this same source shows the following amounts of suitable habitat in each of the states comprising the NRM are, MT. 40924 sq. mi., WY. 29808 sq. mi., ID. 31,586 sq. mi., OR. 2556 sq. mi. and, UT. 1635 sq. mi. This same report indicates that if the 3 major states (ID, MT, and WY) can support 10 BP's for 3 years that the species can be considered to be fully recovered and can be considered for delisting (p.6107 Federal Register). That criteria was met in 2002 (p.6111 Federal Register).

The amount of suitable wolf habitat in the remaining two thirds of the state as depicted in the "Application of habitat models to wolf recovery planning in WA" by Carroll indicates scattered habitat in small isolated areas of the Okanogan, larger amounts of marginal habitat both North and South of Mt. Rainier, and a large area of habitat in and around the Olympic National Park, an area that strongly opposed wolf reintroduction several years ago.

Therefore we feel that the WWG's desired number of BP's is unrealistic given the lack of suitable habitat and the much higher human population density of this state and that the requirement of 15 BP's for 3 years (50% Higher that the USFW criteria for recovery in WY, MT, and ID,) defies common sense. This is further compounded by a recent recommendation

from the Idaho Department of Fish and Game Commissioners to set the limit for a wolf hunt at 2005 levels which could mean 500 wolves could be killed this year. Idaho Fish and Game biologists estimate there are currently about 750 wolves in the state, but after the breeding season this spring they expect more than 1,000. The commissioners on the higher figures because they did not believe that hunting would bring the wolf population numbers down to the levels they wanted to see.

We therefore propose the following numbers of BP's statewide. 3 BP's to down list to Threatened, 6 BP's to down list to State Sensitive, and 8 BP's to change to a Big Game Animal. And we would eliminate the 3 year period since the state was not considered essential for recovery of wolves in the NRM (p.6119 Federal Register).
This total number of 8 BP's or approximately 80 wolves would fit in the states economic analysis as outlined in Chapter XIII, "Economics" which states "Wolf numbers between 50 and 100 animals should pose little detriment to the states livestock industry as a whole…As wolf populations become larger and more widely distributed, financial impacts are likely to accrue to more producers" (p.23 WWG Draft). "Populations of 50 to 100 wolves should not have negative effects on big game hunting in Washington," (p.38 WWG Draft).

The advantages of going with a lower number of BP's are: The sooner wolves can be removed from endangered and threatened status, the more tools stockmen and rural residents will have at their disposal to deal with problem wolves.

The sooner we can get wolves de-listed, the sooner our Fish and Wildlife Department can begin to manage them, until then their hands are tied. The sooner we can get them listed as a Big Game Species, the sooner our Fish and Wildlife can turn them from a liability into an asset through the sale of raffle tags, permits, and Governors Tags.

We believe that these numbers are far too high and do not accurately represent the concerns that the livestock production community has with wolves. The livestock community has preferred zero wolves from the beginning however, due to ESA and WDFW requirements zero is not an option. We support the Minority Opinion Numbers of 3 breeding pairs to downlist to threatened, 6 breeding pairs to downlist to sensitive, and 8 breeding pairs to delist from sensitive and managed as a Big Game Species. The higher numbers that the WWG Draft Plan includes will result in far more individual wolves than Washington has habitat to support thus causing a severe negative impact on private land owners and livestock producers. Livestock producers must be able to protect their property regardless of the wolf's status. We are also concerned that the WDFW has not effectively demonstrated its ability to secure long term funds that will be a requirement in Management and Compensation. Without funding there is **NO Support** of any plan!!

The remainder of the WWG plan is acceptable to the supporters of the minority position.

Jack Field
Jack Field

Duane Cocking
Duane Cocking

Ken Oliver
Ken Oliver

Daryl Asmussen
Daryl Asmussen

Jeff Dawson
Jeff Dawson

Tommie Petrie
Tommie Petrie

MSU researcher shares study on wolf stalking, elk populations at symposium

By ROB CHANEY of the Missoulian | Posted: Friday, November 6, 2009 6:30 am

We guessed right about how many elk wolves eat, but we may have miscalculated how many elk don't get eaten because they don't get born.

That's the conclusion of Montana State University researcher Scott Creel, who spent three years in the Greater Yellowstone Ecosystem. Since wolves were reintroduced there in the 1990s, some elk herds have shrunk by 40 percent to 60 percent, including one in Yellowstone National Park's northern range that went from 17,000 animals to about 6,500.

But it's not that wolves are killing them, Creel said. Rather, the pressure from constant stalking is forcing elk to watch more and eat less.

"Prey animal will do things differently to avoid being killed, and those things aren't free," Creel said. "Their diet changes. They're browsing more and grazing less, that is, eating woody plants instead of grasses. Their nutrition changes as a consequence. In measurements over three winters, we saw their energy intake go down. Pregnancy rates changed as a consequence, so calf-cow ratios dropped pretty dramatically."

Creel noted that his studies applied to Yellowstone and the surrounding mountains, where wolves have made elk their major food source. In the Northern Continental Divide Ecosystem of northwestern Montana, wolves have a more varied diet of deer and elk, and his results might not be repeated there.

Expanding the understanding of wolves and wildlife behavior is a major theme of a two-day symposium of the Society of Conservation Biology's Montana chapter, where Creel was the first speaker on Thursday. Friday's program will bring in researchers and government wildlife managers from Montana, British Columbia and Washington, D.C. Their topics include interactions between bears and wolves, effectiveness of wildlife highway fences, and how to apply science across international borders.

"The great thing about science is everybody gets to throw out their viewpoints," said Ed Bangs, U.S. Fish and Wildlife wolf program coordinator in Helena and one of Friday's presenters. "It isn't like, 'We got the answer - let's go home now.' "

One variation on Creel's research many are interested in is whether the same reduction in pregnancies and calf deliveries holds true for cows and sheep threatened by wolves. Ranchers in wolf-prone parts of Montana have presented anecdotal evidence that their herds are losing weight and pregnancies because of wolf harassment. But Bangs said wolves killing livestock make up less than 1 percent of the state's annual livestock loses.

Another study in play right now is Montana's first-ever wolf big-game hunting season.

Montana hunters have already filled the 12-wolf quota for Wolf Management Unit 3, which includes the Greater Yellowstone Ecosystem and most of southern Montana. As of Friday, they had shot 24 of the allowed 41 wolves in Wolf Management Unit 1, which covers northern Montana above Missoula, Great Falls and Lewistown.

Wolf Management Unit 2, the Bitterroot and Big Hole valleys of southwestern Montana, had 12 of its 22-wolf quota recorded. The season ends Nov. 29, but may be partially extended depending on how many quota kills are unfilled at that point.

RECEIVED
JAN 14 2010
HABITAT PROGRAM

In Idaho, the only other state in the continental United States with a big-game wolf hunt, one district has met its quota and closed. Five more of the state's 12 wolf districts have five or fewer wolves remaining in their quotas. The Idaho season ends Dec. 31 in most areas, but extends to March 31 in two remote districts.

Creel said one difficult aspect of wildlife behavior is whether what we see now is a short-term shift or a long-term trend. In the elk-wolf case, we don't know if elk will adapt new strategies to avoid wolves and recover their numbers, if wolf numbers will fall in conjunction with the shrinking elk herds, or if we've hit a new population balance with wolves on the landscape.

"We don't know what the steady state is," Creel said. "Some of these ecological cycles are a couple decades long."

Reporter Rob Chaney can be reached at 523-5382 or rchaney@missoulian.com.

Posted in Local on *Friday, November 6, 2009 6:30 am Updated: 7:17 am.* | Tags: Wolves

Glucocorticoid stress hormones and the effect of predation risk on elk reproduction

Scott Creel[1], John A. Winnie, Jr., and David Christianson

Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717

Edited by Mark S. Boyce, University of Alberta, Edmonton, Canada, and accepted by the Editorial Board June 12, 2009 (received for review March 3, 2009)

Predators affect prey demography through direct predation and through the costs of antipredator behavioral responses, or risk effects. Experiments have shown that risk effects can comprise a substantial proportion of a predator's total effect on prey dynamics, but we know little about their strength in wild populations, or the physiological mechanisms that mediate them. When wolves are present, elk alter their grouping patterns, vigilance, foraging behavior, habitat selection, and diet. These responses are associated with decreased progesterone levels, decreased calf production, and reduced population size [Creel S, Christianson D, Liley S, Winnie JA (2007) *Science* 315:960]. Two general mechanisms for the effect of predation risk on reproduction have been proposed: the predation stress hypothesis and the predator-sensitive-food hypothesis. Here, we used enzyme immunoassay to measure fecal glucocorticoid metabolite concentrations for 1,205 samples collected from 4 elk populations over 4 winters to test the hypothesis that the effect of predation risk on elk reproduction is mediated by chronic stress. Across populations and years, fecal glucocorticoid concentrations were not related to predator-prey ratios, progesterone concentrations or calf-cow ratios. Overall, the effect of wolf presence on elk reproduction is better explained by changes in foraging patterns that carry nutritional costs than by changes in glucocorticoid concentrations.

antipredator behavior | nonconsumptive effects | risk effect | wolf

Predators affect prey demography through direct predation and through the costs of antipredator behavioral responses, or "risk effects" (1–4). The benefits of antipredator behavior are manifested as a reduction in the rate of direct predation, and these benefits are automatically included when a study measures the direct predation (killing) rate. Risk effects are more difficult to identify and quantify because they are less direct and can be manifest in many ways, but experiments have shown that risk effects can comprise a large proportion of predation's total effect on prey demography and dynamics (5–8). While there is a growing consensus that risk effects are important for predator-prey and food-web dynamics, we still know little about the mechanisms that produce them because few studies have examined all of the steps in the pathway that must exist if risk effects are important for population dynamics—from predation risk to behavioral responses to physiological costs to changes in demography and population dynamics (for an example, see refs. 9–12).

Two general hypotheses have been proposed for the physiological mechanisms that mediate risk effects on the population dynamics of prey. The predator-sensitive food hypothesis suggests that behavioral responses to predators constrain foraging activity or efficiency, and thus strengthen energetic or nutritional constraints on reproduction or survival (13). Many experimental and observational studies have shown that predation risk affects foraging decisions and constraints (14). Fewer studies have tested whether predator-induced changes in foraging patterns carry energetic/nutritional costs or affect prey dynamics, but these relationships can be strong, for example in wildebeest (*Connochaetes taurinus*) in Serengeti National Park and snowshoe hares (*Lepus americanus*) in Kluane National Park (12, 13), but also see ref. 15.

The predation stress hypothesis suggests that exposure to predators causes elevation of glucocorticoid (GC) stress hormones (10, 16–18), which can directly suppress reproduction through effects on the hypothalamic-pituitary-gonadal axis (19, 20), and can indirectly reduce survival and reproduction through effects on the immune and digestive systems (19, 21–23). Experimental studies have shown that exposure to predators or their odors can cause immediate, short-term increases in the circulating GC levels of prey (24–26), but do not always do so (27). Chronic elevation of GCs can interfere with hypothalamic-pituitary-gonadal function, but brief pulses of GC secretion normally do not (19–22). Consequently, experimental studies of short-term responses are important to establish a cause-and-effect relationship between risk and GC responses, but it is also important to test whether natural variation in predation risk is associated with measurable long-term changes in GC levels. Few field studies have examined long-term GC responses to predators, with no clear pattern emerging (10, 16, 28), although 2 recent studies have detected chronic GC responses to predation risk (9, 29).

We have previously shown that mean progesterone concentrations and calf production in Greater Yellowstone Ecosystem (GYE) elk (*Cervus elaphus*) are negatively correlated with the risk of predation by wolves (*Canis lupus*) (30). Elk responded to wolf presence by more than doubling the proportion of daylight hours they spent vigilant (31, 32), and consequently decreasing the proportion of time spent feeding by 19% (33). Elk also responded to wolves by moving into the protective cover of wooded areas when wolves were present, reducing their use of preferred grassland foraging habitats (34–36). Elk strongly prefer grazing to browsing, and habitat type is a strong predictor of the balance of grazing and browsing in elk diets (37). Experiments with GYE elk show that changes in the balance of grazing and browsing affect the rate of mass loss over winter (38). For GYE elk in the Gallatin population, changes in habitat selection and feeding behavior were associated with significant changes in diet and nutrition (38, 39), including a shift from grazing to browsing (39) and a reduction in estimated intake rates by 27% of maintenance requirements (40). GYE elk steadily lose body mass and fat through winter (33, 41), and nutritional condition affects pregnancy rates in elk (42). Elk numbers on GYE winter ranges have declined by as much as 60% since wolf reintroduction (34, 43, 44). For example, elk numbers in Yellowstone's Northern Range herd were between 16,791 and 19,045 in the 3 winters up to 1995, then declined through 11 annual counts to between 6,738 and 6,279 in the 3 winters up to 2008 (45). The decline in GYE elk herds occurred while elk populations in Montana as a whole were growing at a geometric mean annual rate (λ) of 1.030 (46). The decline in GYE elk numbers is larger than can be accounted for by direct predation

Author contributions: S.C., J.A.W., and D.C. designed research; S.C., J.A.W., and D.C. performed research; S.C., J.A.W., and D.C. analyzed data; and S.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.S.B. is a guest editor invited by the Editorial Board.

[1]To whom correspondence should be addressed. E-mail: screel@montana.edu.

rates, and is associated with significant declines in calf-cow ratios immediately after the birth season, and with significantly decreased progesterone concentrations during late gestation (8, 30).

Collectively, these results support the predation-sensitive food hypothesis, but the stress hypothesis remains untested, and the 2 hypotheses are not mutually exclusive (10, 12). In the GYE, elk are exposed to wolves and mount antipredator responses on a near-daily basis (31, 32). The risk of predation is substantial. Given the rate of detected predation (0.08 elk kills per wolf per day) and the ratio of elk to wolves in the populations in this study (287 ± 81, mean ± SEM, $n = 15$ site-year combinations) (30), the per capita probability of predation was 0.21 ± 0.03 annually [mean ± SEM, (note that mean of ratios is greater than ratio of means)]. Like other ungulates, the responses of elk to predators are graded (32), and the most overt antipredator behaviors (rapid fleeing, prancing) are only used during close, direct interactions. However, elk engage in less overt responses such as habitat shifts, reduced feeding, and increased vigilance when wolves are up to 3 km away (32). The cognitive and endocrine correlates of these frequent but subtle changes in behavior are not known, but environmental conditions can elicit a glucocorticoid stress response with little change in overt behavior. For example, the behavioral responses of elk to snowmobiles are much weaker than their behavioral responses to wolves, but their fecal glucocorticoid metabolite (fGCM) concentrations nonetheless increase significantly on days with heavier-than-average snowmobile activity (47).

Experiments with rats suggest that unpredictable or uncontrollable stressors provoke the strongest and most persistent glucocorticoid responses (21, 48), and it is plausible to hypothesize that predation risk is perceived as unpredictable or uncontrollable by elk (and other species) that are exposed to intermittent lethal risk. Here, we test whether (in addition to the nutritional effects described above) fGCM concentrations in elk were associated with predation risk or progesterone levels. Because these data come from the same wolf-elk populations and the same time period as previously published data that detected significant changes in foraging behavior, nutrition, reproductive physiology, demography, and population dynamics, they provide a simultaneous test of the predator-sensitive food and predation-stress hypotheses in a single system.

Results

Contrary to the stress hypothesis, the winter-long mean fGCM concentrations of elk were significantly higher in populations with lower predation pressure (i.e., higher elk-wolf ratios: Fig. 1*A*; $b = 0.13 \pm$ SE 0.059, Wald 5.00, $P = 0.025$). The interpretation of this result is not simple, for 2 reasons. First, the result is highly dependent on data from a single population in a single year (Fig. 1*A*). If this high-leverage data point is removed there is no detectable relationship between winter-long fGCM concentrations and elk-wolf ratios. Second, plasma steroid binding globulins with a high affinity for progesterone also have high affinity for corticosteroids (49). Consequently, circulating total cortisol concentrations often rise in parallel with progesterone concentrations in the final trimester of gestation, and this increase in circulating cortisol is typically accompanied by an increase in fecal corticosteroid metabolite concentrations (50). The expected late-gestation rise in fGCM concentration has previously been reported for elk (51, 52) and is apparent in our data for all site-years. Fecal GC concentrations notably increased after 15 March (Fig. 2), when elevated progesterone levels can be used to diagnose pregnancy (30). To test whether increased fGCM concentration in late winter could be explained on the basis of increased binding globulin levels that accompany the third trimester rise in progesterone, we examined temporal variation in fGCM concentration for a set of fecal samples from individuals of known sex. For randomly-collected samples not sorted by sex, fGCM concentration increased significantly during the winter [general linear model (GLM) fit by maximum likelihood, $b = 0.64 \pm 0.14$, Wald statistic = 20.97, $P < 0.0001$]. This seasonal rise was strongly apparent in samples from females (Fig. 2: GLM fit by maximum likelihood, $b = 0.70 \pm 0.18$, Wald statistic = 14.72, $P < 0.0001$), but was weak or absent in samples from males (Fig. 2: GLM fit by maximum likelihood, $b = 0.32 \pm 0.19$, Wald statistic = 2.90, $P = 0.09$).

These results suggest that late-gestation samples from pregnant females should be excluded from analyses that test the

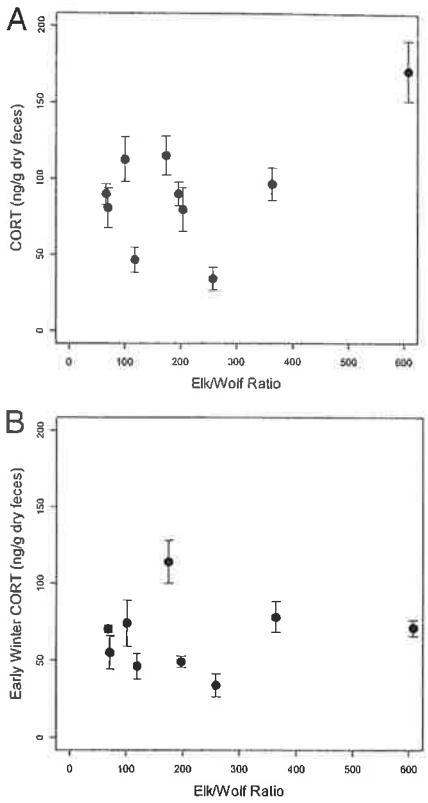


Fig. 1. Relationship of mean fGCM concentration to predation pressure, as measured by elk-wolf ratios. Units of analysis are population-years. Whiskers show standard errors. (*A*) Winter-long mean fGCM concentration. (*B*) Early winter mean fGCM concentration [samples collected prior the increase in progesterone after 15 March (see Fig. 2)].

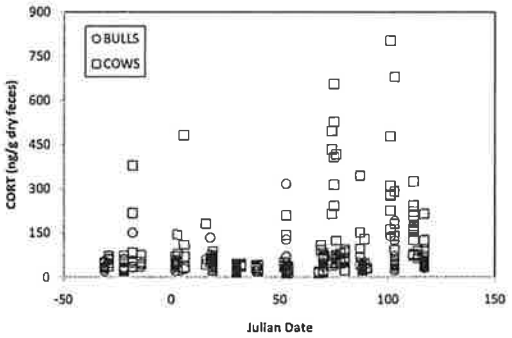


Fig. 2. fGCM concentrations rise after 15 March (Julian Date = 74), concurrent with significant increases in progesterone concentration at the onset of the third trimester of gestation. This seasonal rise in fGCM concentration is apparent in samples from females (squares) but not males (circles), and can be explained by the late gestational increase in plasma steroid binding globulins in females.

response of cortisol to potential stressors such as predation risk. This caveat is especially important for comparisons of fGCM concentration levels among groups that vary in their pregnancy rates, as is the case here (30). In particular, the result shown in Fig. 1*A* was strongly leveraged by the high fGCM concentration for 1 site-year, for which the estimated pregnancy rate was 100%. To avoid the potentially confounding effect of late-gestation changes while testing for a relationship between cortisol and predation pressure, we regressed early winter (before 15 March) fGCM concentration on elk-wolf ratios, and found no relationship (Fig. 1*B*; $b = 0.01 \pm$ SE 0.044, Wald 0.059, $P = 0.808$). By either test, fGCM did not correlate positively with predation risk as predicted by the stress hypothesis (Fig. 1 *A* and *B*).

Also contrary to the stress hypothesis, neither progesterone levels nor calf recruitment were detectably related to fGCM concentration (Fig. 3*A*, regression of progesterone on winter-long mean fGCM concentration: $b = 1.10 \pm$ SE 3.24, Wald = 0.114, $P = 0.73$; Fig. 3*B*, regression of subsequent calf-cow ratio on winter-long fGCM concentration: $b = 0.017 \pm$ SE 0.074, Wald = 0.050, $P = 0.82$, Fig. 3*C*, regression of progesterone on early winter fGCM concentration: $b = 4.38 \pm$ SE 5.64, Wald = 0.598, $P = 0.44$; regression of subsequent calf-cow ratio on early winter fGCM concentration: $b = 0.041 \pm$ SE 0.013, Wald = 0.095, $P = 0.76$). Finally, there were no significant negative correlations between progesterone and fGCM concentration for individuals within single populations or population-years.

Density dependence is not a plausible explanation for low progesterone and calf recruitment in the populations with high predation risk because reproduction declined as these populations declined in size following wolf recolonization (30, 43). As expected, given this general pattern, population density was not a strong driver of fecal progesterone or fGCM concentrations (progesterone slope is of incorrect sign, $b = 854.7 \pm$ SE 512.0, Wald = 2.79, $P = 0.10$) (fGCM slope is of incorrect sign, $b = -9.14 \pm$ SE 45.98, Wald = 0.039, $P = 0.84$) (Fig. 4).

Discussion

Risk effects can be an important part of the total impact of predation on prey dynamics (5, 6, 53). Risk effects can also cascade to affect community composition and ecosystem function (2, 7, 54, 55). For elk, exposure to wolf predation is associated with changes in grouping patterns (56, 57), habitat selection (34, 35), vigilance (31–33), foraging (33), diet (39, 58), nutrition (38–40, 58), reproductive physiology (30), and demography (8, 30). Elk populations in the GYE (and elsewhere e.g., Banff National Park) have decreased in size since wolf recolonization, while elk populations in neighboring areas with low wolf density grew steadily as a result of weak limitation by winter snowfall (43, 45, 46, 59). Measured rates of direct predation are too low to explain the observed changes in elk calf production and population size (8), and radio-tagging of newborn calves reveals little direct predation by wolves in the first several months of life (30, 60). Collectively, these results strongly suggest a nonconsumptive risk effect of wolves on elk dynamics.

Our data suggest that the nonconsumptive effect of wolves on elk reproductive physiology and calf recruitment is not mediated by chronic activation of the GC stress response. Prior research shows that the effect of predation risk on elk reproduction is associated with changes in nutrition. Elk in Yellowstone steadily lose body mass and body fat throughout winter (33, 41), and when the body fat of elk drops below 12%, the probability of maintaining pregnancy declines rapidly (42). In the presence of wolves, we found a decrease in the proportion of time spent foraging, a shift from grazing to browsing, and a substantial reduction in the rate of intake (33, 24, 39). Together with the results presented here, the data suggest that the effect of wolf presence on elk reproduction is mediated by nutritional effects, and is not mediated by a chronic GC response.

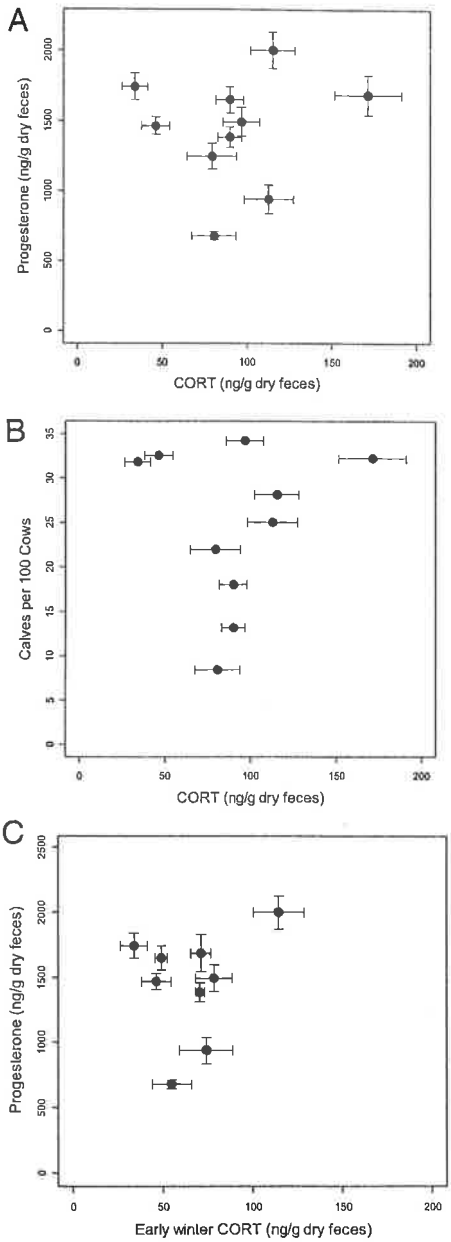


Fig. 3. Relationships of mean fecal progesterone concentration and calf recruitment in the subsequent year to mean fGCM concentration. (*A*) Relationship of fecal progesterone concentration to winter-long fGCM concentration. (*B*) Relationship of subsequent calf-cow ratios to winter-long fGCM concentration. (*C*) Relationship of fecal progesterone concentration to early-winter fGCM concentration

Chronic elevation of GCs can have many pathological consequences (19, 21, 22), including shifts in metabolic pathways that mobilize energy in the short term, but reduce metabolic efficiency. Consequently, it might be expected that prey would not mount GC responses to predators, if encounters with predators are an everyday event, as they are for Yellowstone elk and many other species in intact ecosystems. Because elk have consistently negative energy budgets and steadily lose body mass during winter plant dormancy (37), any physiological response to wolves that reduced winter-long metabolic efficiency should be disfavored by natural selection. We still know little about the psycho-neuro-endocrinology of antipredator responses (24, 25), but

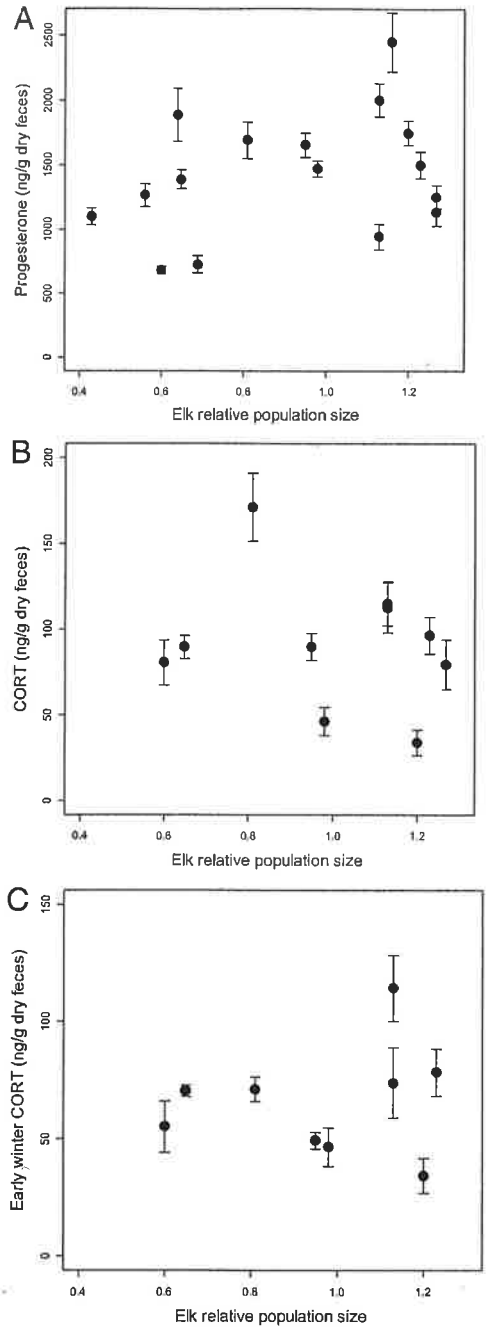


Fig. 4. Mean fecal progesterone and glucocorticoid metabolite concentrations were not detectably related to changes in population density. Relative population density was measured as a population's current size divided by the long-term mean size of that population, so that a value of one indicates a population at its long-term mean density. (*A*) Fecal progesterone concentration. (*B*) Winter-long mean fGCM concentration. (*C*) Early winter mean fGCM concentration.

psychological stressors generally cause strong and persistent glucocorticoid responses when they involve unpredictable or uncontrollable upsets to homeostasis (19, 21). Elk typically detect wolves and take action to reduce their risk; perhaps these behavioral responses avoid or diminish hypothalamic-pituitary-adrenal responses so that there is no detectable effect of risk on GC concentrations at the population level, even though mean progesterone levels declined by a factor of 2.5 in the same set of fecal samples (30). We did not test for short-term GC responses, and our data are compatible with the hypothesis that immediate encounters with predators produce GC responses that are small enough, or brief enough, that they do not detectably alter mean GC concentrations, but it is unlikely that such GC responses would interfere with progesterone secretion and the maintenance of pregnancy.

The cognitive and emotional aspects of avoiding predation remain unknown in this case, as in virtually all studies of "the ecology of fear" (58, 61). Many authors implicitly or explicitly assume that risk effects are mediated by stress or fear, and the term "predation stress" is becoming a synonym for "predation risk" (62, 63), but it should be remembered that risk effects can logically arise through mechanisms that do not involve the stress response. Our failure to detect a long-term GC response does not prove that elk do not fear wolves. By the same token, a demonstration that elk avoid wolves need not imply that fear drives the response. Females of many species avoid mates of low quality, but do they fear them? Vegetarians avoid meat, but do they fear it?

Materials and Methods

We collected data from elk on 4 winter ranges within the GYE, for 1–4 winters (2002–2006) at each site. The 4 sites are at similar elevation, with mixtures of coniferous forest and sage-steppe. Elk migrate from these winter ranges to higher elevation sites in the summer, but studies using radio-telemetry and ear-tagging have detected little movement between populations during the winter (34, 64); movement between sites would require an elk to cross one or more alpine passes with deep snow.

Elk were counted and herd compositions were recorded in aerial total counts conducted by the Montana Department of Fish, Wildlife, and Parks during winter, when elk aggregate at predictable low-elevation locations and are more easily detected due to high contrast with the snowy environment. Methods for these aerial surveys are described in detail elsewhere (46). Wolf numbers come from distribution maps and pack size tallies in US Fish and Wildlife Service annual reports, based on aerial radiotracking to locate packs that were then counted by direct observation. Methods for quantifying wolf numbers are described in Fish and Wildlife Service annual reports for the Northern Rocky Mountains Wolf Recovery Project (available at http://www.fws.gov/mountain-prairie/species/mammals/wolf/). For 4 years on the Gallatin site, we had independent data from near-daily observations, which confirmed the above numbers.

For fGCM determinations, we collected fresh elk fecal pellets from the snow and stored them at −40 °C in screw top vials. For each winter range, we collected 3–10 samples per sampling occasion, stratified at 2 week intervals throughout the winter (December 1–May 15). We analyzed 1,205 samples from 10 site-year combinations. When resting elk stand up, they frequently defecate in a discrete pile of pellets within the snow crater they have created, and these individual defecation sites are easily distinguished by snow tracking. We collected 10 pellets from each individual defecation site that we sampled. The fecal pellets of calves and adults differ significantly in size (39), and we avoided collecting samples from calves. The adult sex ratio of elk populations is consistently female-biased, and adult females comprised 73% of these populations (including calves), so the samples primarily represent the endocrine responses of adult females. Nonetheless, we tested for effects of variation in the adult sex ratio on hormone concentrations by calculating the proportion of the population that was composed of adult females for each site in each year, using aerial count data. This proportion ranged from 0.67–0.83, and none of the inferences we report were altered by the inclusion of sex-ratio as a covariate.

We homogenized each sample, dried ≈1g of homogenate with a rotary evaporator, and extracted steroids from ≈200 μg of dried feces (weighed to 0.01 mg) by boiling in ethanol. We dried extracts under forced air and reconstituted them with 1 mL 95% methanol for storage at −80 °C. With these extracts, we assayed cortisol at 36-fold methanol dilution with a monoclonal double-antibody enzyme immunoassay (R&D Systems KGE008). This cortisol antibody has <4.4% cross reactivity with other steroids (1.7% for progesterone). Binding curves for serial dilution of extracts and cortisol standards were parallel from 156–10,000 pg/mL. Recovery of cortisol added to extracts was 1.02 ± 0.03 (mean ± SEM). Intra-assay and interassay coefficients of variation were 5.26% and 7.31%. Sensitivity was 2 orders of magnitude below the minimum concentration of diluted fecal extracts. For biological validation, we compared concentrations to those we obtained with an RIA previously vali-

dated for elk feces by corticotropin challenge (65) for 232 samples, and found a close correlation [$r^2 = 0.90$, $RIA = 184 + 3.8$ enzyme immunoassay (EIA) $-0.011\,EIA^2$]. Because this EIA employs a monoclonal cortisol antibody, our fecal fGCM concentrations are measured as ng CORT immunoreactivity/g dry feces, although circulating glucocorticoids are enzymatically modified during biliary excretion, with 11-17-dioxoandrostanes predominating in ruminant feces (50, 51).

Methods for progesterone enzyme immunoassay and procedural validation data have been published previously (30). We restricted progesterone determinations to samples collected after 15 March, when elevated progesterone can be used to detect pregnancy. Overall, the mean pregnancy rate [determined by fecal progesterone >830 ng/g dry feces (30)] averaged 85% for these populations. For biological validation, we compared pregnancy detection via fecal EIA with detection via serum pregnancy-specific protein B for 30 samples collected from the same individuals on the same day. This comparison yielded 93.3% sample-concordance, with identical population pregnancy rates. We also compared pregnancy detection by EIA to results from a previously validated progesterone RIA (66), with 94.3% sample-concordance and $r^2 = 0.95$ for 35 samples. We further tested the EIA's repeatability by drying, extracting and assaying 38 samples twice (in a blind manner), yielding 95% concordance in one-sample pregnancy diagnoses and $r^2 = 0.74$ for concentrations. Finally, we tested repeatability by determining the pregnancy rate in 2 independent sets of fecal samples ($n = 38$ and 50) from the same population and year. These rates agreed to <1%.

Circulating cortisol levels commonly increase during gestation because the plasma binding globulin for progesterone also has strong affinity for cortisol (49). Consequently, we determined whether our tests might be affected by late gestational increases in steroid binding globulins of females, but not males. To do this, we used a set of 177 fecal samples from individuals of known gender (see *Results*, Fig. 2).

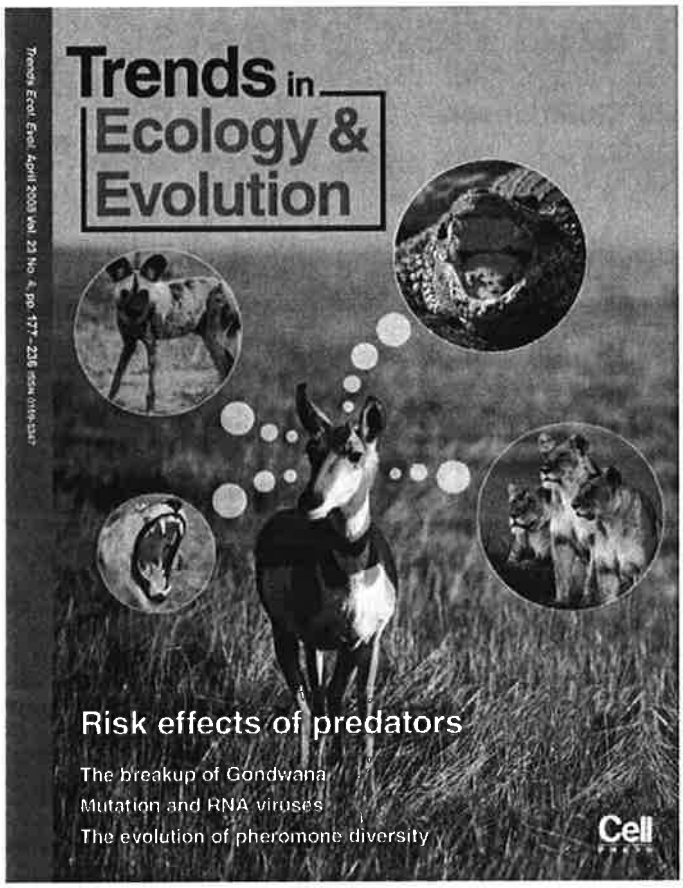
We used maximum likelihood to fit general linear models with normal errors and an identity link, unless stated otherwise with results. Assumptions were tested by visually checking residual distributions and Q-Q plots. After log-transformation, elk-wolf ratios met the assumption of normality of residuals. The analyses we report use unweighted means, but no inferences changed when we fit models weighted by sample size or the inverse of variance. Finally, no reported inferences changed when we fit more complex mixed models that included variation among populations as a random effect.

ACKNOWLEDGMENTS. We thank Stewart Liley for his excellent work in the field and laboratory; Yellowstone National Park and the Montana Department of Fish, Wildlife, and Parks for permission to conduct the research and logistical assistance. This work was funded by grants from Animal Behavior program of the National Science Foundation.

1. Peckarsky BL, Cowan CA, Penton MA, Anderson C (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74:1836–1846.
2. Schmitz, OJ, et al. (2008) From individuals to ecosystem function: Toward an integration of evolutionary and ecosystem ecology. *Ecology* 89:2436–2445.
3. Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecol Lett* 7:153–163.
4. Sih A (1992) Prey uncertainty and the balancing of antipredator and feeding needs. *Amer Nat* 139:1052–1069.
5. Pangle KL, Peacor SD, Johannsson OE (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology* 88:402–412.
6. Preisser EL, Bolnick DI, Blumstein DT (2005) Scared to death? The effects of intimidation and consumption in predator prey interactions. *Ecology* 86:501–509.
7. Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
8. Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends Ecol Evol* 23:194–201.
9. Sherriff MJ, Krebs CJ, Boonstra R (2009) The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *J Anim Ecol* advanced online doi: 10.1111/j.1365–2656.2009.01552.x.
10. Boonstra R, Hik D, Singleton GR, Tinnikov A (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecol Monogr* 68:371–394.
11. Boonstra R, Singleton G (1993) Population declines in the snowshoe hare and the role of stress. *Gen Comp Endocrinol* 91:126–143.
12. Krebs CJ, et al. (1995) Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
13. Sinclair ARE, Arcese P (1995) Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology* 76:882–891.
14. Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014.
15. Mduma SAR, Sinclair ARE, Hilborn R (1999) Food regulates the Serengeti wildebeest: A 40-year record. *J Anim Ecol* 68:1101–1122.
16. Clinchy M, Zanette L, Boonstra R, Wingfield JC, Smith JNM (2004) Balancing food and predator pressure induces chronic stress in songbirds. *Proc R Soc London Ser B* 271:2473–2479.
17. Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Cons Ecol* 6:11.
18. Lima SL (1998) Stress and decision-making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Adv Stud Behav* 27:215–290.
19. Romero LM (2004) Physiological stress in ecology: Lessons from biomedical research. *Trends Ecol Evol* 19:249–255.
20. Moberg GP (1991) How behavioral stress disrupts the endocrine control of reproduction in domestic animals. *J Dairy Sci* 74:304–311.
21. Sapolsky RM (2002) *Behavioral Endocrinology*, eds Becker JB, Breedlove SM, Crews D, McCarthy MM (MIT Press, Cambridge) pp 409–450.
22. Sapolsky RM (2005) The influence of social hierarchy on primate health. *Science* 308:648–652.
23. Munck A, Guyre PM, Holbrook NJ (1984) Physiological functions of glucocorticoids in stress and their relation to pharmacological actions. *Endocrinol Rev* 5:25.
24. Cockrem JF, Silverin B (2002) Sight of a predator can stimulate a corticosterone response in the great tit (*Parus major*). *Gen Comp Endocrinol* 125:248–255.
25. Monclus R (2005) Behavioural and physiological responses of naive European rabbits to predator odour. *Anim Behav* 70:753–761.
26. Thaker M, Lima SL, Hews DK (2009) Alternative antipredator tactics in tree lizard morphs: Hormonal and behavioural responses to a predator encounter. *Anim Behav* 77:395–401.
27. Ylönen H, Eccard JA, Jokinen I, Sundell J (2006) Is the antipredatory response in behaviour reflected in stress measured in faecal corticosteroids in a small rodent? *Behav Ecol Sociobiol* 60:350–358.
28. Scheuerlein A (2001) Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). *Proc R Soc London Ser B* 268:1575–1582.
29. McCormick MI (2009) Indirect effects of heterospecific interactions on progeny size through maternal stress. *Oikos* 118:744–752.
30. Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315:960.
31. Creel S, Winnie J, Jr, Christianson D, Liley S (2008) Time and space in general models of antipredator response: Tests with wolves and elk. *Anim Behav* 76:1139–1146.
32. Liley S, Creel S (2008) What best explains vigilance in elk: Characteristics of prey, predators, or the environment? *Behav Ecol* 19:245–254.
33. Winnie J, Creel S (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim Behav* 73:215–225.
34. Creel S, Winnie J, Maxwell B, Hamlin KL, Creel M (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
35. Fortin D, et al. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
36. Kauffman MJ, et al. (2007) Landscape heterogeneity shapes predation in a newly restored predatorprey system. *Ecol Lett* 10:690–700.
37. Christianson D, Creel S (2007) A review of environmental factors affecting winter elk diets. *J Wildl Manage* 71:164–176.
38. Christianson D, Creel S (2009) Effects of grass and browse consumption on winter mass dynamics of elk. *Oecologia* 158:603–613.
39. Christianson D, Creel S (2008) Risk effects in elk: Sex-specific response in grazing and browsing due to predation risk from wolves. *Behav Ecol* 19:1258–1266.
40. Christianson D, Creel S (2009) A nutritionally-mediated risk effect of wolves on elk. *Ecology*, in press.
41. Cook RC, Cook JG, Mech LD (2004) Nutritional condition of northern Yellowstone elk. *J Mammal* 85:714–722.
42. Cook RC, Murray DL, Cook JG, Zager P, Monfort SL (2001) Nutritional influences on breeding dynamics in elk. *Can J Zool* 79:845–853.
43. White PJ, Garrott RA (2005) Yellowstone's ungulates after wolves—Expectations, realizations, and predictions. *Biol Cons* 125:141–152.
44. Beyer HL, Merrill EH, Varley N, Boyce MS (2007) Willow on Yellowstone's northern range: Evidence for a trophic cascade? *Ecol Appl* 17:1563–1571.
45. White PJ (2008) *2007–2008 Annual Winter Trend Count of Northern Yellowstone Elk* (Yellowstone Center for Resources, Yellowstone National Park, WY).
46. Hamlin KL (2004) *Montana Elk Management Plan* (Montana Fish, Wildlife & Parks, Helena, MT).
47. Creel S, et al. (2002) Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Cons Biol* 16:809–814.
48. Weiss JM (1970) Somatic effects of predictable and unpredictable shock. *Psychosom Med* 32:397–408.
49. Breuner CW, Orchinik M (2002) Plasma binding proteins as mediators of corticosteroid action in vertebrates. *J Endocrinol* 175:99–112.
50. Touma C, Palme R (2005) Measuring fecal glucocorticoid metabolites in mammals and birds: the importance of validation. *Ann New York Acad Sci* 1046:54–74.
51. Huber S, Palme R, Arnold W (2003) Effects of season, sex, and sample collection on concentrations of fecal cortisol metabolites in red deer (*Cervus elaphus*). *Gen Comp Endocrinol* 130:48–54.
52. Millspaugh JJ, et al. (2001) Fecal glucocorticoid assays and the physiological stress response in elk. *Wildl Soc Bull* 29:899–907.
53. Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.

54. Frank DA (2005) The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia* 143:629–634.
55. Frank DA (2008) Evidence for top predator control of a grazing ecosystem. *Oikos* 117:1718–1724.
56. Creel S, Winnie JA (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim Behav* 69:1181–1189.
57. Hebblewhite M, Pletscher DH (2002) Effects of elk group size on predation by wolves. *Can J Zool* 80:800–809.
58. Hernandez L, Laundre JW (2005) Foraging in the "landscape of fear" and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildl Biol* 11:215–220.
59. Hebblewhite M, Pletscher D, Paquet PC (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Can J Zool* 80:789–799.
60. Barber SM, Mech LD, White PJ (2005) Yellowstone elk calf mortality following wolf restoration: Bears remain top summer predators. *Yellowstone Sci* 13:37–44.
61. Brown JS, Laundre JW, Gurung M (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *J Mammal* 80:385–399.
62. Relyea RA, Mills N (2001) Predator-induced stress makes the pesticide carbaryl more deadly to gray treefrog tadpoles (*Hyla versicolor*). *Proc Natl Acad Sci* 98:2491–2496.
63. Stoks R (2001) Food stress and predator-induced stress shape developmental performance in a damselfly. *Oecologia* 127:222–229.
64. Brazda AR (1953) Elk migration patterns, and some of the factors affecting movements in the Gallatin River drainage, Montana. *J Wildl Manage* 17:9–23.
65. Wasser SK, et al. (2000) A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocrinol* 120:260–275.
66. Garrott RA, Monfort SL, White PJ, Mashburn KL, Cook JG (1998) One-sample pregnancy diagnosis in elk using fecal steroid metabolites. *J Wildl Dis* 34:126–131.

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Opinion

Cell PRESS

Relationships between direct predation and risk effects

Scott Creel and David Christianson

Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717, USA

Risk effects arise when prey alter their behavior in response to predators, and these responses carry costs. Empirical studies have found that risk effects can be large. Nonetheless, studies of predation in vertebrate conservation and management usually consider only direct predation. Given the ubiquity and strength of behavioral responses to predators by vertebrate prey, it is not safe to assume that risk effects on dynamics can be ignored. Risk effects can be larger than direct effects. Risk effects can exist even when the direct rate of predation is zero. Risk effects and direct effects do not necessarily change in parallel. When risk effects reduce reproduction rather than survival, they are easily mistaken for limitation by food supply.

Predation risk effects are common and can be strong, but are rarely considered in conservation or wildlife management

Predators affect prey demography through direct predation and through the costs of antipredator behavioral responses, or risk effects [1,2] (Figure 1). Responses to risk can be morphological [3] or behavioral [4], including changes in habitat use [5–7], vigilance [8,9], foraging [10,11], aggregation [12,13], movement patterns [14–16] and sensitivity to environmental conditions [17]. The costs of these responses can be manifest by reduced survival, growth or reproduction [1,18–20] (Figure 2). Recent empirical research has shown that risk effects on prey dynamics can be as large as direct effects, or even larger [15,18,21,22]. Although such research has established that risk effects can be an important part of the total effect of predation, many analyses of predation as a limiting factor still consider only direct effects, particularly in studies focusing on conservation and management, and particularly in studies of vertebrates (e.g. [23–25]). When risk effects *are* considered, many analyses focus on effects that cascade from the prey to other species [26–29], rather than effects on the prey species itself [2] (Figure 3). Perhaps risk effects are often ignored in this context (risk effects are well studied in other contexts) simply because there is no general theory for the expected relative magnitudes of direct and risk effects, or for the expected relationship between the two.

Here we use a simple conceptual model to examine two questions about the expected relationship between direct predation and risk effects. First, do direct effects or risk effects comprise the larger portion of the total effect of predation? Second, how are direct effects and risk effects correlated? If risk effects are small and positively related to direct effects, then measurements of direct predation rates should provide a good estimate of the total effect of predators on prey. This is the assumption implicit in many studies of predation in natural systems. However, if risk effects are large and negatively related to direct effects, then measurements of direct predation could be unrelated or negatively related to the total effect of predation, a hypothesis that remains largely untested. Without considering this possibility, it would be easy to mistake risk effects for bottom-up limitation, particularly when risk reduces the reproductive rate, rather than increasing mortality [1,2,19]. For example, analyses of snowshoe hare dynamics originally suggested that predation affects survival, but reproduction is controlled by density-dependent access to food. When Boonstra *et al.* [2] extended prior analysis to consider risk effects, they found that 'predation risk, not high hare density or poor nutritional condition, accounted for...the marked deterioration of reproduction during the decline phase' (p. 371).

Are direct effects or risk effects expected to comprise the larger portion of the total effect of predation?

Empirical studies have recently shown that the risk effects of predation can be large, sometimes substantially larger than direct effects. For example, Pangle *et al.* [18] estimated direct effects and risk effects of predatory spiny water fleas (*Bythotrephes longimanus*) on three species of zooplankton in Lake Michigan and Lake Erie, and found that over six combinations of location and depth, risk effects on population growth rates were more than seven times larger than the effect of direct predation. Nelson *et al.* [21] amputated the mouthparts of predatory damselbugs (*Nabis* spp) so they could not kill their prey (pea aphids, *Acyrthosiphon pisum*). Comparing treatments with manipulated and normal predators, they found that risk effects accounted for 39%–80% of the total impact of predation on prey population growth. Schmitz *et al.* [15] used this approach with predatory spiders (*Pisurina mira*) and grasshopper prey (*Melanoplus femurrubrum*), and found that 'risk spiders' caused the same level of grasshopper mortality as normal, lethal spiders.

Despite such empirical studies (and many others [22]), we have no general theory to predict whether these should be common results. We suggest that the logic by which the principle of allocation is applied to life-history trade-offs can also be applied to this question. In life-history theory, reproductive value is the sum of current fecundity and

Corresponding author: Creel, S. (screel@montana.edu).

0169-5347/$ – see front matter © 2007 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2007.12.004 Available online 4 March 2008

Author's personal copy

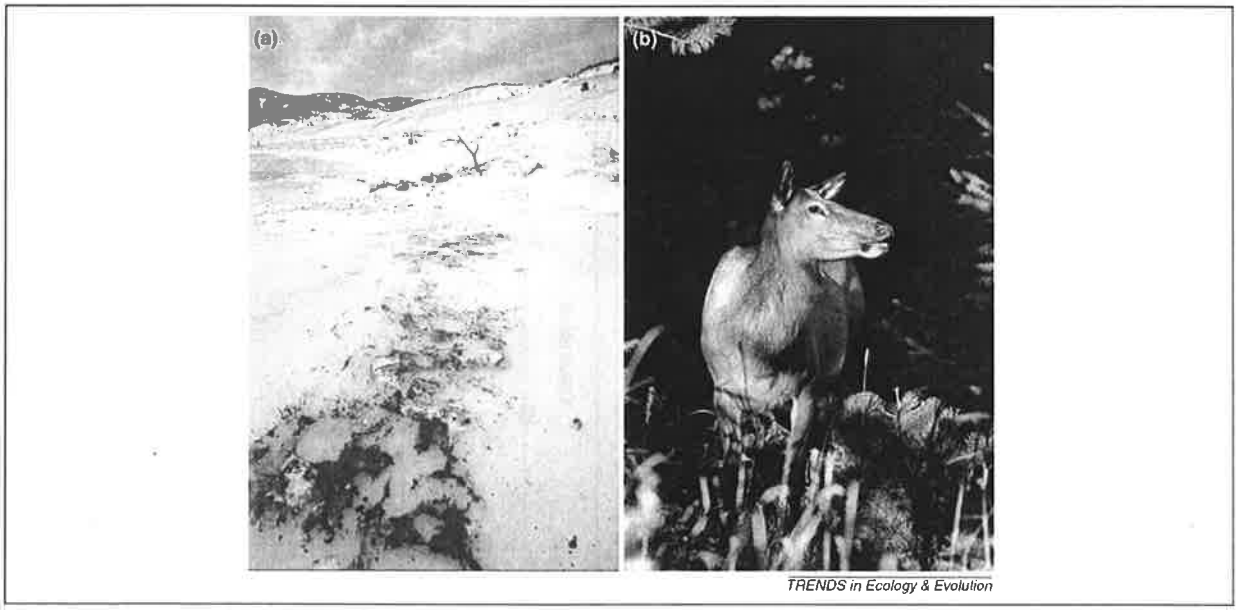


Figure 1. To understand the total effect of predation on prey populations, we must understand the relative importance of direct predation **(a)** and risk effects, which are the costs of antipredator behaviors that reduce direct predation but carry fitness costs, such as vigilance and retreat to safe habitats **(b)**.

residual reproductive value, and the shape of the curve relating residual reproductive value to current reproductive effort determines the optimal trade-off between a fitness benefit and its opportunity cost. Similar logic can be used to examine trade-offs between direct predation and risk effects. Figure 4 shows several ways that direct and risk effects might be related. Generally, as the effort invested in antipredator behavior increases, risk effects will increase and direct predation will decline. If an increase in antipredator behavior is equally effective at reducing direct predation for any level of antipredator response, then the trade-off curve would be linear. Evolutionary logic suggests that the slope of a linear trade-off should be −1. Positive slopes would quickly be eliminated by selection, because they represent a situation in which antipredator behavior *increases* the rate of direct predation. Behavioral responses that yielded a linear fitness trade-off with any negative slope other than −1 would also be eliminated by selection, because selection would favor individuals who decreased direct effects to zero (for slopes steeper than −1) or decreased risk effects to zero (for slopes shallower than −1), reducing such cases to a single point on one of the axes. The case of pure direct costs might not be surprising, but the case of pure risk effects raises the important point that predation might affect prey fitness (and thus dynamics) even in the absence of direct killing.

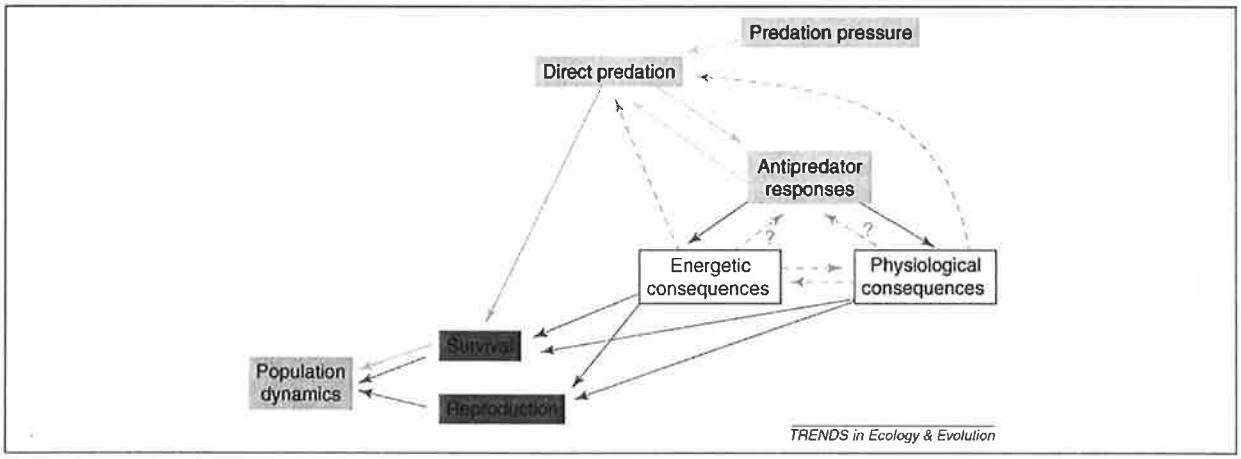


Figure 2. Pathways by which predation can affect the population dynamics of prey: the restricted view that predation operates only through direct offtake is illustrated by two orange arrows linking predation rates to prey dynamics by way of survival; this is only the tip of the iceberg. Pink boxes and arrows illustrate that direct predation rates are not simply an external ecological force imposed on prey by predators, but are determined jointly by the intensity of predation pressure and the antipredator response of prey to that pressure. This creates a feedback loop between direct predation and antipredator responses. In turn, antipredator responses can have physiological or energetic costs for prey, which could alter prey dynamics via either reproduction or survival. These risk effects are illustrated by blue arrows, with likely feedbacks illustrated by gray arrows.

Author's personal copy

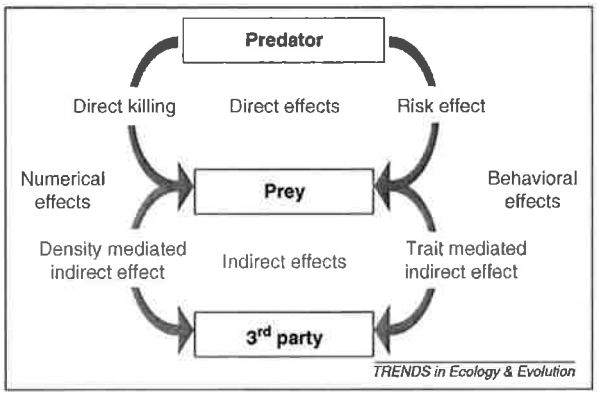


Figure 3. A classification of predation effects into four basic types using two dichotomies: numerical effects of predation operate through changes in prey numbers. Numerical effects are well studied, both as direct killing and as density-mediated indirect effects. Indirect effects are traditionally defined as effects that cascade from the predator to the prey and on to a third species. Although studies of behavioral responses to predation risk are common, the effects of risk on population and community dynamics have received much less attention. Trait-mediated indirect effects have (surprisingly) received more attention than risk effects. Risk effects are often called 'sublethal' or 'nonlethal' effects, although they can be lethal. Risk effects are also called 'fear effects,' although few studies actually test the hypothesis that fear drives antipredator responses. More care is warranted with the connotations of these terms.

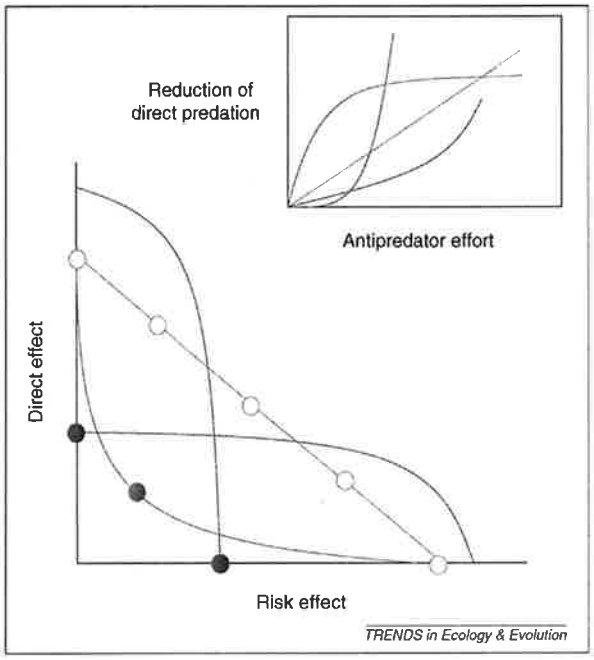


Figure 4. The relative magnitudes of fitness costs manifest as direct predation or as risk effects: one can imagine several reasonable relationships between the demographic cost of direct predation (direct effect on fitness) and the demographic cost of avoiding predation (risk effect on fitness). The inset figure shows the effectiveness with which antipredator effort reduces direct predation, for each of the fitness trade-off curves in the main figure (matched by color). For these trade-off curves, natural selection will favor strategies that minimize the total cost of predation, which is the sum of the fitness costs of direct predation and risk effects. Solid points identify the strategy that minimizes the total cost of predation for trade-off curves with asymptotic benefits of antipredator behavior (green) or accelerating benefits of antipredator behavior (red and blue). Open points identify multiple strategies that yield equal total costs of predation, if antipredator behavior has constant benefits, which yields a linear trade-off curve with slope −1 (orange). For these trade-off curves, the costs of direct predation and risk effects must be measured in the same units, ideally total fitness. In practice, both fitness costs will usually be measured by changes in demographic components of fitness such as rates of survival or reproduction. Note that risk effects can comprise from 0% to 100% of the total effect of predators on prey.

We will return to this point. For the case of linear trade-offs with slope −1, any level of antipredator behavior yields the same total effect of predation. Both risk effects and direct effects are expected, but we cannot predict their relative magnitudes.

The curvature of fitness cost-benefit curves has been shown to be an important determinant of the way that prey should optimize trade-offs between predation risk and starvation risk [30], and curvature is also important here (for similar reasons). For example, it is possible that antipredator responses are initially effective at reducing direct predation, but then yield diminishing returns with increasing effort, as might be the case for antipredator vigilance [31]. In this case, the trade-off curve for direct predation and risk effects would be concave-up (Figure 4, green curve): consequently, both direct and risk effects are expected. It is also possible that antipredator behavior is initially ineffective at reducing direct predation, but antipredator responses become more effective as the level of response increases, as could be the case for antipredator changes in patterns of grouping [32], particularly when prey disaggregate into smaller groups to avoid detection [11,33]. In this case, the trade-off curve would be concave-down (Figure 4, red and blue curves): consequently, the total cost of predation is expected to be either completely direct (Figure 4, red curve) or completely indirect (Figure 4, blue curve). Concave-down trade-off curves with different shapes show that prey species with very different direct predation rates might experience equal total effects of predation (even if one species has a direct predation rate of zero).

To summarize, the manner in which antipredator behavior reduces direct predation should determine the shape of the trade-off curve for direct and risk effects, which helps to predict the expected magnitudes of the effects. Many ecological studies implicitly assume that when direct predation rates are low, the total effect of predation is necessarily weak, but this assumption is questionable, because risk effects can logically be larger than direct effects. McNamara and Houston [30] used a simple model of trade-offs between starvation and predation to reach a similar conclusion, that "the number of animals that die from starvation may not provide a reliable indication of the importance of food" (p. 1515).

How are direct effects and risk effects expected to be correlated?

Ecologists concerned with identifying which factors most strongly limit a population (for example by comparing the effects of food, predators and weather) often measure the direct rate of predation and ignore risk effects when assessing the impact of predators on prey. This traditional approach implicitly assumes that direct effects are larger than risk effects, or that risk effects (typically unmeasured) correlate positively with direct effects. Empirical studies and the conceptual model above suggest that the first assumption is often not safe. Is it any safer to assume that risk effects are always positively correlated with direct effects?

Author's personal copy

If the level of attempted predation on a prey species is driven mainly by the decisions of the predator, and not by the prey, then direct effects and risk effects could be positively related (Figure 5a). This is a logical expectation for comparisons on an ecological timescale, over which there are no evolutionary changes in the shape of the trade-off curve relating risk effects to direct predation. For example, consider a comparison among several populations of a single prey species that are exposed to different densities of their primary predator. A high rate of attempted predation would favor strong expression of antipredator responses, in comparison to a population with a low rate of attack, and this would produce a positive association between direct predation and risk effects (Figure 5a).

This argument, however, assumes that the antipredator behavior does not reduce the rate of predation. Feedback between antipredator behavior and the rate of predation will tend to eliminate or reverse the positive relationship between direct predation and risk effects. To illustrate this point, consider an example in which a predator attacks prey species *A* and *B* equally often, and both prey have the same level of antipredator response. If *A* increases its level of antipredator behavior effectively, and predation pressure consequently shifts to *B*, then direct effects and risk effects would become negatively correlated. This scenario seems plausible, particularly for situations in which a predator chooses from a set of morphologically similar prey of comparable sizes. As Figure 5b illustrates, evolutionary changes in the trade-off between direct predation and risk effects (as tested by comparisons between species, or between the sexes within a species) should also produce negative correlations. To summarize, predation pressure mediated only by the predator should produce a positive relationship between direct and risk effects, whereas predation pressure that is modified by prey responses should reduce this correlation or produce negatively correlated effects.

In summary, risk effects can be large in comparison to the effect of direct predation, and the correlation between risk effects and direct predation need not be positive. If risk effects are not explicitly considered, they could easily be mistaken for limitation by food supply, particularly in observational studies and particularly when they are manifested as reductions in reproduction (as shown in snowshoe hares, arctic ground squirrels, elk, bluegill sunfish and several invertebrates [1,2,19,34,35]). Logically, if one does not consider risk effects, then predation can be expected to affect prey dynamics only through survival, so decreased reproduction will probably be attributed to another limiting factor, such as food supply.

Given these possibilities, measurements of the total effect of predation on prey dynamics should consider risk effects (Box 1). Why have risk effects been ignored in most studies that relate the impacts of predation to other limiting factors? First, there are the common assumptions that risk effects must be smaller than direct effects and positively related to them. Second, risk effects are the product of hundreds or thousands of small actions, with individually small effects on fitness that eventually add up, whereas direct predation is a dramatic event with

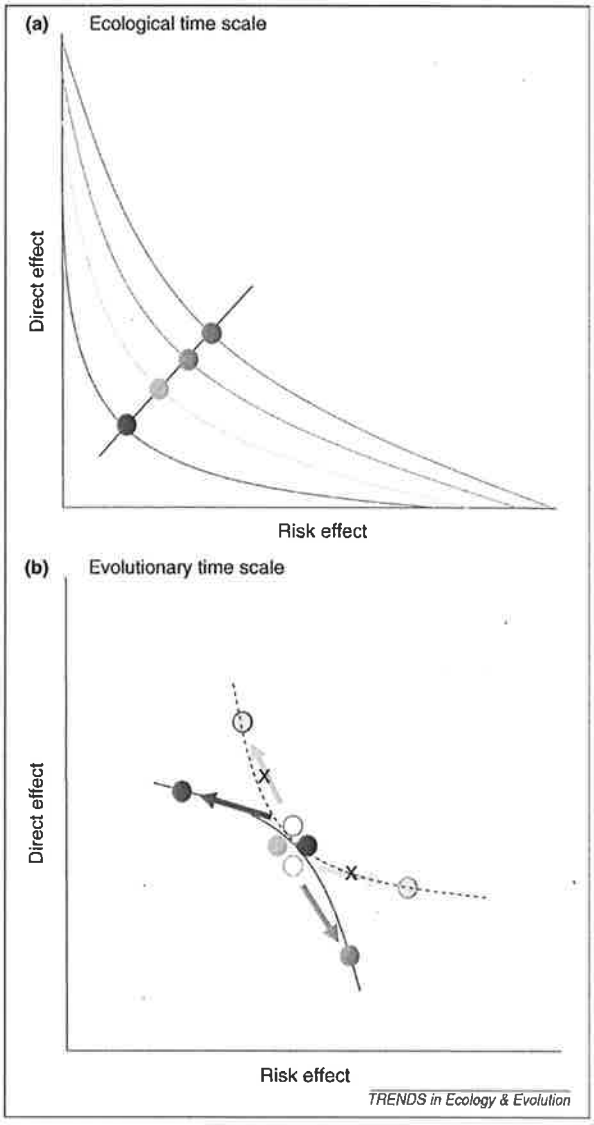


Figure 5. Possible correlations between risk effects and direct effects of predation: **(a)** considers the likely relationship between risk effects and direct predation rates on an ecological timescale, over which there are no evolutionary changes in the shape of the trade-off curve relating risk effects to direct predation (see Figure 1). This logic would apply, for example, to a comparison of multiple populations of a single prey species that faced varying levels of predation pressure from a given predator. As direct predation pressure increases (from the red curve to the blue curve), the optimal balance of risk and predation effects (identified by solid points) causes risk effects to also increase. Consequently, a positive correlation between direct predation and risk effects (black line) is expected. **(b)** considers the likely relationship between risk effects and direct predation rates over evolutionary timescales. The four central points represent four ancestral prey species with similar antipredator behavior and morphology, with similar direct predation rates and risk effects. A behavior arises in one species (open green point) that allows a large reduction in direct predation with little increase in the risk effect (dark green arrow to solid green point). A different behavior arises in another species (open blue point) that allows a large reduction in antipredator effort with little increase in direct predation (dark blue arrow to solid blue point). Both of these behaviors reduce the total cost of predation and would consequently be favored by natural selection. The result is a negative correlation between risk effects and direct predation rates, across the set of four prey species. The lighter blue and green arrows/points indicate new behaviors that would increase the total cost of predation, and thus would not be favored by natural selection. Comparing the favored and disfavored possibilities suggests that negative correlations between risk effects and direct predation (for evolutionary comparisons across species) can have concave-down shapes.

Author's personal copy

Box 1. Risk effects and predator–prey dynamics

To illustrate the potential effects of antipredator behavior on predator–prey dynamics, consider an extension of the Lotka-Volterra equations [39]:

$$N_{t+1} = \frac{N_t \lambda}{1 + aN_t^b} - eP_tN_t \qquad P_{t+1} = \frac{feP_tN_t - dP_t}{1 + a'P_t^{b'}}$$

Here, prey numbers (N_t) are controlled by their finite rate of increase (λ), two parameters that describe density dependence (a,b), and by direct predation (eP_tN_t). Direct predation depends on the numbers of predators (P_t) and prey (N_t), which determine the likelihood that an encounter will occur, and the efficiency (e) with which predators make a kill upon encountering prey. Predator (P_t) population dynamics are also density dependent (with parameters a' and b'), but the finite rate of increase is decomposed into a death rate in the absence of prey (d) and a birth rate that depends on two variables: the efficiency with which predators kill prey (e) and a factor (f) that converts each prey item killed into a demographic impact on the predator's growth rate (f is large for prey of high net energetic value). In Figure I, this model is applied with parameter values that mimic elk and wolf dynamics in the Gallatin Canyon population of the Yellowstone ecosystem [6,11].

In most discussions of predator–prey dynamics, the impact of predation is evaluated by direct offtake (in this model, ePN) [23,40–43]. The basic results of these models are well known: as direct offtake increases (via e), a tendency toward a joint equilibrium is replaced by damped, stable and expanding cycles (compare Figures Ia and Ib). However, more novel results emerge if we examine risk effects, or population dynamics that incorporate explicit costs of antipredator behavior. To isolate risk effects in a simple way, consider a scenario in which predation pressure increases but offtake does not increase, because prey respond with an increase in antipredator behavior (vigilance [11], aggregation [33] or redistribution [6,16]). As the level of antipredator behavior increases, we assume that it carries increasing costs. Intuitively, the simplest manner to incorporate these costs is by decreasing the rate of prey population growth (λ), independent of prey density (Figure Ic). This approach assumes that energy is limiting and that antipredator responses require an increase in energy expenditure and/or reduced foraging efficiency. At this stage of the argument, the effect on λ could be manifest through survival or fecundity. The critical point is this: when antipredator behavior causes a reduction in λ, population dynamics become more stable (Figure Ic versus Ia). This is in sharp contrast to an increase in direct predation, which is destabilizing (Figure Ib versus Ia). The picture is complicated by considering that another effect of antipredator behavior might be to increase the strength of density dependence in the prey population, rather than simply decreasing λ in a density-independent manner. Stronger density dependence could arise if prey concentrate in low-risk habitats or aggregate in larger herds. Figure Id differs from Figure Ia through a 25% change in the value of b, which shifts from under-compensating to compensating density dependence in the absence of predation. In this case, an increase in the cost of predator avoidance destabilizes the dynamics (Figure Id versus Figure Ia or Ic).

These simple (but plausible) scenarios show that the costs of antipredator behavior can have complex effects on predator–prey dynamics (also shown by other models [26,44–46]). Although the parameter values above were tailored to elk and wolves on a given study site (Box 2), we do not imply that this model realistically describes wolf–elk dynamics. The model is a tool to highlight the importance of measuring demographic risk effects, and ultimately incorporating these costs into models of predator–prey dynamics [26], which has not previously been considered in the models used to evaluate the quantitative effects of wolves on elk dynamics [23,24,47,25]. This is fundamentally an empirical issue, because the optimal responses by elk depend on the costs and effectiveness of antipredator behavior, processes that we cannot expect to predict by logic alone. Theory does not cleanly reveal the balance between predation risk and the cost of antipredator behavior for a given species.

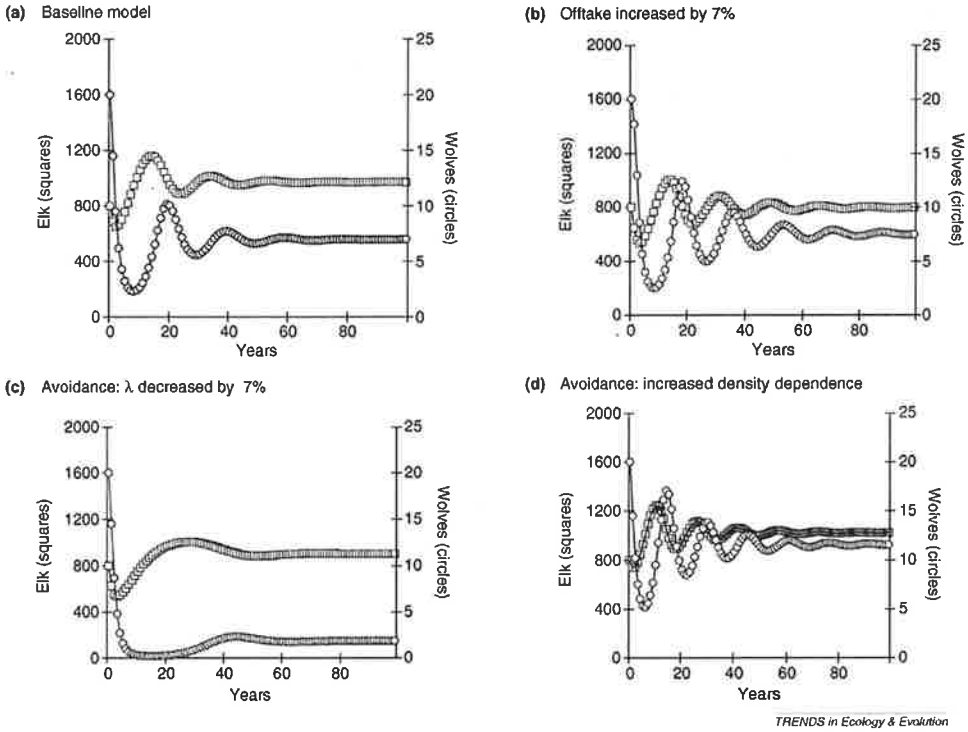


Figure I. Predator–prey dynamics with variation in direct offtake and risk effects. Adding risk effects to a simple model of predator–prey dynamics does not have the same effect as increasing direct offtake, and different types of risk effects alter dynamics in different ways.

Author's personal copy

immediately obvious effects on fitness. Finally, even once one has established a research focus on risk effects, it is very difficult to isolate and measure the impact of behavior on demography and dynamics, because behavior and demography change on very different timescales. (Of course, the direct predation rate can itself be hard to measure in practice, although the challenges are conceptually simpler. Radiotracking and direct observation of predators or prey can yield good estimates of direct predation rates [35–37]. Most other approaches do not allow estimation of the direct predation rate, and consequently aggregate direct predation and risk effects into a total effect of predation, without distinguishing between the two mechanisms.)

Measuring risk effects

Risk effects on prey dynamics have been quantified in several ways. To date, most research has used experimental approaches. One of the most productive lines of research has employed experimental studies with manipulated predators. Peckarsky *et al.* [1], Schmitz *et al.* [15] and Nelson *et al.* [21] conducted very revealing experiments by gluing together the mouthparts of invertebrate predators, and comparing the impacts of lethal and 'risk-only' predators on prey demography [1], density [15] and population dynamics [21]. These seminal experiments have played a central role in identifying risk effects, and in demonstrating that risk can account for a large proportion of the total impact of predators on prey [22]. Still, experiments in captivity with manipulated predators leave room to wonder how the results generalize to natural conditions.

Large-scale field experiments with snowshoe hares (*Lepus americanus*) [2,38] and arctic ground squirrels (*Spermophilus parryii plesius*) [35,36] have combined food supplementation and predator exclosures (as in Werner *et al.*'s [34] classic experiments on fish) to show that when combined, food limitation and predation had more-than-additive effects on population density. Exclosure of predators increased the density of both hares [2] and squirrels [35], largely by increasing reproduction (a risk effect). The more-than-additive effects of predation and food limitation is also consistent with risk effects, because a given level of antipredator response is likely to carry larger demographic costs when animals are in poor condition (and see Figure 5a). This result would also arise if food limitation forces prey to reduce antipredator behavior, increasing their vulnerability to predation. For example, Winnie and Creel [11] showed that male elk, with significantly lower fat stores than females, mounted weaker antipredator responses to wolves than females did, despite facing higher per capita predation risk.

Small-scale experiments that manipulate the lethality of predators and field experiments that manipulate food supply and exposure to predators have been central to understanding risk effects. Still, a major challenge and opportunity remains to develop field studies measuring the relative magnitudes of direct predation and risk effects in the wild, without manipulations that could alter their relative magnitudes. Pangle *et al.* [18] recently demonstrated a promising approach, estimating direct and risk effects for two zooplankton prey (*Daphnia* and *Bosmina*) using a combination of field data on antipredator responses and experimental data on the demographic costs of these responses. Box 2 suggests another possible method to

Box 2. A challenge and an opportunity: measuring risk effects in field studies

To illustrate the difficulties of estimating the magnitudes of risk effects and direct predation using observational data, consider wolf–elk interactions. Since the reestablishment of wolf predation on the Gallatin elk winter range in the Yellowstone ecosystem, the proportion of female elk entering winter with a calf has declined by more than a factor of two (Figure I). In parallel, the population has declined [6], although most Montana elk populations simultaneously grew strongly during this period [48]. Much of the decline in Gallatin calf recruitment can be attributed to reduced reproduction. The progesterone levels of female elk declined significantly with increasing wolf:elk ratios, and these changes in progesterone were significantly correlated with changes in calf recruitment [19]. For Gallatin elk, the calf:cow ratio immediately after the annual birth pulse has declined by 39% since wolf recolonization. These changes in reproduction were associated with strong changes in female elk behavior [11], habitat selection [6], grouping [33] and sensitivity to environmental conditions [17]. Reduced calf numbers after the birth pulse account for a decline of 17.3 calves/100 cows (Figure I). Increased bear predation on very young calves could potentially contribute to this decline, by increasing the number of calves killed before they can be counted. Contrary to this hypothesis, summer calf:cow ratios were not detectably related to estimated bear density (general linear model: Wald statistic = 0.004, $P = 0.95$, using breeding bear numbers in Yellowstone National Park [49]), whereas wolf presence remains a strong predictor of summer calf:cow ratios after controlling for the potential effect of bears and snow accumulation during the gestation period (GLM: Wald statistic = 6.12, $P = 0.013$). Grizzly bear numbers in the Yellowstone ecosystem have increased mainly by population expansion, but the density of breeding bears within the ecosystem core has not changed detectably (Figure 5 in Ref. [49]).

How does the impact of risk on elk reproduction compare to the impact of direct calf predation? Calf survival from birth to early winter has declined by 37% from the pre-wolf period to the post-wolf period, but this decline in survival cannot be neatly attributed to direct predation or risk effects. At least in principle, it is a combination of the two. Even if all of the change in calf survival from the pre-wolf period to the post-wolf period was due to direct wolf predation (i.e. no risk effects on calf survival), this would account for a decline of only 6.3 calves/100 cows. (In Figure I, 6.3 is the difference between the pre-wolf and post-wolf periods for the decrease in calf:cow ratios from summer to winter.) Radiotelemetry of wolves [37] and elk calves [19] has been used to directly estimate the rate of predation. In the winter, observations of Gallatin wolf kills yield a direct predation rate of 0.030 calves killed/wolf/day, closely comparable to the rate of 0.027 calves killed/wolf/day for a neighboring population [37]. If this winter predation rate applied also to summer and fall, then wolves on the Gallatin site would kill an average of 74 calves in 180 days between birth and early winter. (Note that studies of radiotagged elk calves show lower rates of wolf predation in summer/fall than in winter, but do not allow precise estimates of the rate [19].) Direct killing of 74 calves accounts for a decline of 9.0 calves/100 cows, given the size of the Gallatin herd ($X \pm \text{SEM} = 1138 \pm 86$ elk, 1996–2006) and the proportion that are adult females (72%).

Thus, for elk calf recruitment, risk effects on reproduction were ~2–3 times larger than the effect of direct predation (17.9 versus 6.3 to 9.0 calves/100 cows), and the total effect of predation on recruitment was ~3–4 times larger than was captured by measures of direct predation.

Author's personal copy

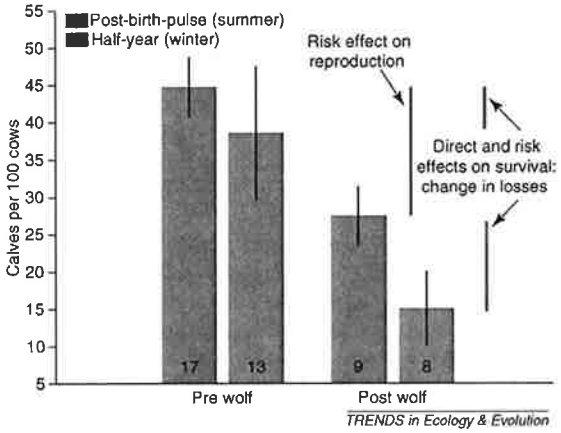


Figure I. Wolf predation and elk calf number: elk dynamics are strongly affected by calf recruitment, and the proportion of females entering winter with a calf has declined significantly ($t_{17} = 5.12$, $P < 0.0001$) since the reestablishment of wolf predation on the Gallatin elk winter range in the Yellowstone ecosystem. A large proportion of this decline in winter calf recruitment can be attributed to reduced reproduction (a risk effect), as revealed by a significant drop in calf:cow ratios immediately following the summer birth pulse ($t_{23} = 6.79$, $P < 0.0001$). The sum of direct wolf predation and risk effects on calf survival are manifest as changes in survival rates from birth to 6 months for the pre-wolf and post-wolf periods. Bars show means; whiskers show 95% confidence intervals. Numbers within bars are sample sizes (annual surveys).

compare the demographic costs of direct predation and risk effects, using observational data from the wild.

Conclusions

The benefit of antipredator behavior is a decreased risk of predation, and this is automatically incorporated into measures of the direct rate of predation. By contrast, most analyses of vertebrate predator–prey dynamics do not account for the costs of antipredator behavior (risk effects). Logically, risk effects can be larger than the effects of direct predation. By the same logic, risk effects can be either negatively or positively correlated with direct effects, depending on the type of comparison being made. Excellent experimental studies of a broad range of species have confirmed that risk effects on prey demography, density and dynamics can be large, sometimes exceeding direct effects. If risk effects are not considered explicitly, it seems likely that they will go undetected or be attributed to processes other than predation, particularly when risk effects reduce reproduction. The challenge now is to design field studies that determine the relative magnitudes of risk effects and direct predation in wild populations that are not manipulated. Finally, risk effects are becoming well recognized in pure ecology, but are still largely ignored in the fields of conservation and management. It is important that measurement of risk effects penetrates into work on predation as a limiting factor in problems of conservation and wildlife management.

Acknowledgements

John Winnie and Stewart Liley made many important contributions to our thinking on these issues in the course of our research on wolves and elk. This work was supported by a grant from the National Science Foundation Animal Behavior Program. Jim Estes and three anonymous referees made many helpful suggestions on the manuscript.

References

1 Peckarsky, B.L. *et al.* (1993) Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74, 1836–1846
2 Boonstra, R. *et al.* (1998) The impact of predator-induced stress on the snowshoe hare cycle. *Ecol. Monogr.* 68, 371–394
3 Tollrian, R. and Harvell, C.D. (1999) The evolution of inducible defenses: current ideas. In *The Ecology and Evolution of Inducible Defenses* (Tollrian, R. and Harvell, C.D., eds), pp. 306–321, Princeton University Press
4 Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48, 25–34
5 Anholt, B.R. and Werner, E.E. (1999) Density-dependent consequences of induced behavior. In *The Ecology and Evolution of Inducible Defenses* (Tollrian, R. and Harvell, C.D., eds), pp. 218–230, Princeton University Press
6 Creel, S. *et al.* (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397
7 Hebblewhite, M. *et al.* (2005) Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144
8 Childress, M.J. and Lung, M.A. (2003) Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Anim. Behav.* 66, 389–398
9 Armitage, K.B. (2004) Badger predation on yellow-bellied marmots. *Am. Midl. Nat.* 151, 378–387
10 Lima, S.L. and Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659
11 Winnie, J., Jr and Creel, S. (2007) Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim. Behav.* 73, 215–225
12 Boesch, C. (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117, 220–242
13 Barta, Z. *et al.* (2004) The effects of predation risk on the use of social foraging tactics. *Anim. Behav.* 67, 301–308
14 Sih, A. and McCarthy, T.M. (2002) Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Anim. Behav.* 63, 437–443
15 Schmitz, O.J. *et al.* (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399
16 Fortin, D. *et al.* (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330
17 Winnie, J., Jr *et al.* (2006) Elk decision-making rules are simplified in the presence of wolves. *Behav. Ecol. Sociobiol.* 61, 277–289
18 Pangle, K.L. *et al.* (2007) Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology* 88, 402–412
19 Creel, S. *et al.* (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315, 960
20 Ruxton, G.D. (1997) Predator-induced breeding suppression and its consequences for predator-prey population dynamics. *Proc. Biol. Sci.* 264, 409–415
21 Nelson, E.H. *et al.* (2004) Predators reduce prey population growth by inducing changes in prey behavior. *Ecology* 85, 1853–1858
22 Preisser, E.L. *et al.* (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86, 501–509
23 Eberhardt, L.L. *et al.* (2003) Assessing the impact of wolves on ungulate prey. *Ecol. Appl.* 13, 776–783
24 White, P.J. and Garrott, R.A. (2005) Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biol. Cons.* 125, 141–152
25 Varley, N. and Boyce, M.S. (2006) Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecol. Model.* 193, 315–339
26 Bolker, B. *et al.* (2003) Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology* 84, 1101–1114
27 Werner, E.E. and Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100
28 Luttbeg, B. *et al.* (2003) Prey state and experimental design affect relative size of trait- and density-mediated indirect effects. *Ecology* 84, 1140–1150

Author's personal copy

29 Dill, L.M. *et al.* (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* 84, 1151–1157
30 McNamara, J.M. and Houston, A.I. (1987) Starvation and predation as factors limiting population size. *Ecology* 68, 1515–1519
31 Pulliam, H.R. (1973) On the advantages of flocking. *J. Theor. Biol.* 38, 419–422
32 Caro, T. (2005) *Antipredator Defenses in Birds and Mammals,* University of Chicago Press
33 Creel, S. and Winnie, J.A., Jr (2005) Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Anim. Behav.* 69, 1181–1189
34 Werner, E.E. *et al.* (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64, 1540–1548
35 Karels, T.J. *et al.* (2000) The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. *J. Anim. Ecol.* 69, 235–247
36 Byrom, A.E. *et al.* (2000) Experimental manipulation of predation and food supply of arctic ground squirrels in the boreal forest. *Can. J. Zool.* 78, 1309–1319
37 Smith, D.W. *et al.* (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *J. Wildl. Manag.* 68, 153–166
38 Krebs, C.J. *et al.* (1995) Impact of food and predation on the snowshoe hare cycle. *Science* 269, 1112–1115
39 Volterra, V. (1926) Variations and fluctuations of the numbers of individuals in animal species living together. *Mem. R. Accad. Naz. dei Lincei* (translated in Chapman, R. [1931] *Animal Ecology,* McGraw-Hill)
40 Abrams, P.A. and Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* 15, 337–341
41 Eberhardt, L.L. (2000) Reply: predator-prey ratio dependence and regulation of moose populations. *Can. J. Zool.* 78, 511–513
42 Hayes, R.D. and Harestad, A.S. (2000) Wolf functional response and regulation of moose in the Yukon. *Can. J. Zool.* 78, 60–66
43 Messier, F. and Joly, D.O. (2000) Comment: regulation of moose populations by wolf predation. *Can. J. Zool.* 78, 506–510
44 Abrams, P.A. and Matsuda, H. (1997) Prey adaptation as a cause of predator-prey cycles. *Evolution Int. J. Org. Evolution* 51, 1742–1750
45 Ives, A.R. and Dobson, A.P. (1987) Antipredator behavior and the population dynamics of simple predator-prey systems. *Am. Nat.* 130, 431–447
46 Luttbeg, B. and Schmitz, O.J. (2000) Predator and prey models with flexible individual behavior and imperfect information. *Am. Nat.* 155, 669–683
47 Boyce, M.S. (1995) Anticipating consequences of wolves in Yellowstone: model validation. In *Ecology and Conservation of Wolves in a Changing World* (Carbyn, L.C. *et al.*, eds), pp. 199–209, Canadian Circumpolar Institute
48 Hamlin, K.L. (2004) *Montana Elk Management Plan.* Montana Fish, Wildlife & Parks
49 Schwartz, C.C. *et al.* (2006) Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildl. Monogr.* 161, 1–68

Have you contributed to an Elsevier publication? Did you know that you are entitled to a 30% discount on books?

A 30% discount is available to all Elsevier book and journal contributors when ordering books or stand-alone CD-ROMs directly from us.

To take advantage of your discount:

1. Choose your book(s) from www.elsevier.com or www.books.elsevier.com

2. Place your order

Americas:
Phone: +1 800 782 4927 for US customers
Phone: +1 800 460 3110 for Canada, South and Central America customers
Fax: +1 314 453 4898
author.contributor@elsevier.com

All other countries:
Phone: +44 (0)1865 474 010
Fax: +44 (0)1865 474 011
directorders@elsevier.com

You'll need to provide the name of the Elsevier book or journal to which you have contributed. Shipping is free on prepaid orders within the US.

If you are faxing your order, please enclose a copy of this page.

3. Make your payment

This discount is only available on prepaid orders. Please note that this offer does not apply to multi-volume reference works or Elsevier Health Sciences products.

For more information, visit www.books.elsevier.com

Author's personal copy

ANIMAL BEHAVIOUR, 2008, 76, 1139–1146
doi:10.1016/j.anbehav.2008.07.006

Available online at www.sciencedirect.com
ScienceDirect

Time and space in general models of antipredator response: tests with wolves and elk

SCOTT CREEL, JOHN A. WINNIE, JR, DAVID CHRISTIANSON & STEWART LILEY
Department of Ecology, Montana State University, Bozeman

(Received 25 March 2008; initial acceptance 28 April 2008; final acceptance 17 June 2008; published online 13 August 2008; MS. number: A08-00204)

Considerable research has tested two axioms about antipredator behaviour: prey may respond to temporal variation in risk (the risky times hypothesis) or to spatial variation in risk (the risky places hypothesis). The risk allocation hypothesis extends the risky times hypothesis, noting that the context into which a period of risk or safety is imbedded should affect the level of response, and predicting that vigilance should be greatest during a brief pulse of risk and lowest during a brief pulse of safety. We tested these models using natural variation in true predation risk, by observing elk, *Cervus elaphus*, in the presence or absence of wolves, *Canis lupus*, on three sites in the Greater Yellowstone Ecosystem, over 4 winters. Elk were exposed to wolves frequently in the Northern Range, intermittently in the Gallatin Canyon, and never in the Elkhorn Mountains. We used GLM to control the effects of herd size and composition while testing for responses of vigilance to daily wolf presence (temporal variation) and to site-specific, background levels of risk (spatial variation). The data gave strong support to the risk allocation hypothesis and equivocal support to the risky times hypothesis, and did not support the risky places hypothesis. Contrary to the risky places hypothesis but as predicted by risk allocation, Gallatin elk were more vigilant than Northern Range elk despite lower background risk in the Gallatin Canyon. The contradictory predictions of the risk allocation and risky places hypotheses have important ramifications for research on the ecological consequences of antipredator behaviour.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: *Canis lupus*; *Cervus elaphus*; elk; predation; risk allocation hypothesis; risk effect; vigilance; wolf; Yellowstone

In ecological studies, predation risk is often treated as a parameter that varies among places, by measuring some index of risk across space and asking how spatial variation in risk affects the distribution, abundance or survival of prey animals (Hebblewhite et al. 2002; Kauffman et al. 2007; Frid et al. 2008). Ecological studies of predation risk are often observational, relying on natural but uncontrolled variation in the location of real predation risk. When risk is mapped onto space, temporal variation in risk is often ignored, making the implicit assumption that short-term behavioural responses to risk are adequately predicted by the long-term pattern of risk associated with a site.

Correspondence: S. Creel, Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717, U.S.A. (email: screel@montana.edu).

In contrast, behavioural studies often treat predation risk as a parameter that varies through time, by measuring changes in levels of vigilance, grouping, movement or habitat selection in the immediate presence or absence of a predator (Lima & Dill 1990). Studies of behavioural responses to risk are often experimental, with controlled exposure to temporal variation in predator cues that induce responses by the prey, but with no real risk of predation. Behavioural observations or experiments often do not consider spatial variation in risk, although some do, often focusing on spatial variation within one immediate location, rather than variation among distinct locations (Werner et al. 1983; Lima 1990) Both of these broad approaches have proven very useful, but considering variation in risk across both space and time simultaneously can yield inferences that differ from those based only on spatial or temporal variation (Mitchell & Lima 2002; Creel & Winnie 2005).

0003–3472/08/$34.00/0
© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Author's personal copy

Moreover, Lima & Bednekoff (1999) have clarified logical expectations about the responses of prey to temporal variation in risk, noting that 'temporal variability in risk leaves animals with the problem of allocating feeding and antipredator efforts across different risk situations ... the nature of this temporal variation itself can fundamentally influence antipredator decision making'. In essence, their 'risk allocation hypothesis' predicts that the optimal response to a pulse of risk or safety depends on the sequence in which the pulse is imbedded. Assuming that antipredator vigilance trades off with foraging (as it does for elk, *Cervus elaphus*; Winnie & Creel 2007), the risk allocation hypothesis predicts that vigilance will be greatest during a pulse of risk within a background of safety (because there is a high probability that safer feeding conditions will soon arise) and lowest during a pulse of safety within a background of risk (because there is a high probability that more dangerous feeding conditions will quickly return). These predictions are subtly but importantly different from the predictions of other hypotheses about responses to risk. One alternative, the 'risky times hypothesis', considers temporal variation in risk, but in a simpler manner than the risk allocation hypothesis. The risky times hypothesis simply suggests that prey will increase their vigilance when predators are present, regardless of the background sequence of risk and safety for their location. Another alternative, the 'risky places hypothesis', hypothesizes that prey use the long-term risk level of their location to make decisions about their level of vigilance. The risky places model of antipredator behaviour is implicitly assumed by most recent studies of elk antipredator behaviour and ecology (Wolff & Van Horn 2003; Childress & Lung 2003; Fortin et al. 2005; Kauffman et al. 2007), because they relate the behaviour of elk to variation across sites in the long-term risk of predation, but they do not explicitly consider temporal variation of risk within a site. Simplest is the null model, which predicts that prey maintain a constant level of vigilance that is not sensitive to temporal or spatial variation in risk.

The risk allocation hypothesis has been tested in several experiments with simulated risk (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk et al. 2002; Pecor & Hazlett 2003; Sundell et al. 2004). These tests have shown that prey follow the risk allocation strategy under some conditions, but apparently not always. To our knowledge, no field study has yet tested the risk allocation hypothesis with vertebrate prey exposed to natural variation in real predation risk in a manner that distinguishes between the risk allocation, the risky times and the risky places hypotheses (see Griffin et al. 2005 for a field test that supports risk allocation but is also compatible with risky times). Field tests are important, because natural risk does not switch abruptly on and off in the simple, dichotomous manner of most experimental tests. Moreover, many species (particularly vertebrates) can probably perceive the difference between real and simulated risk and adjust their behavioural responses (e.g. Kruuk 2002, page 172). For example, the difference between true predation and simulated risk is probably relevant when considering habituation as a possible explanation for a weak antipredator response. Well-designed experiments with strong inference have shown us that animals are *capable* of using the risk allocation strategy to adjust their responses to temporal variation in risk, but they do not reveal whether risk allocation is an important strategy under natural circumstances or is overwhelmed by other factors.

Perhaps more important, the predictions of the risk allocation and risky places hypotheses are directly contradictory, a point that is not widely appreciated. The risk allocation hypothesis makes the counterintuitive prediction that optimal vigilance levels should be lower in locations with a higher proportion of time spent at risk, whether predators are immediately present or absent (Fig. 1; also see Figure 3 of Lima & Bednekoff 1999). This prediction directly opposes the primary prediction of the risky places hypothesis, so risk allocation and risky places cannot both be correct. (We will return to this point in the Discussion, to elaborate a point that is important for comparison of these models with field data: such comparisons must recognize that the original formulation of the risk allocation model assumes that average levels of vigilance are the same for all of the situations being compared. That is, Lima & Bednekoff 1999 modelled a situation in which average vigilance was the same for the situations being compared: the allocation of vigilance to different periods was free to vary, but overall mean vigilance levels were not free to vary.) Recognizing the fundamental differences in the predictions of these general models could have broad and important ramifications for studies of the ecological

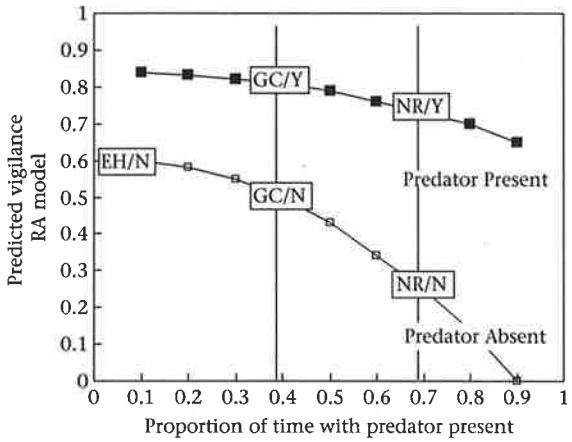


Figure 1. Predicted levels of vigilance from the risk allocation hypothesis for elk in three populations that vary in the frequency of days that wolves were locally present (Y) or absent (N). Despite less frequent exposure to wolves, Gallatin Canyon (GC) elk are predicted to be more vigilant than Northern Range (NR) elk, both when wolves are present and when they are absent. This counterintuitive prediction arises because the risk allocation hypothesis predicts a negative relationship between vigilance levels and the proportion of time spent at risk, for periods of both immediate risk (upper line) and safety (lower line). Elk in the Elkhorn Mountains (EH) were not exposed to wolves. The quantitative values of vigilance (ordinate) depend on the details of parameters in the risk allocation model that we do not discuss: only the qualitative pattern is meaningful. This pattern is taken directly from the original formulation of the risk allocation model (Lima & Bednekoff 1999).

Author's personal copy

consequences of variation in predation among locations, for example, in studies of local predator losses or reintroductions.

We tested the predictions of these hypotheses by measuring the vigilance levels of elk in the immediate presence and absence of wolves, *Canis lupus*, on three sites in the Greater Yellowstone Ecosystem, which varied in the frequency at which wolves were locally present. Wolves were widely distributed at high density on the Northern Range (NR) site, so elk experienced relatively continuous risk with pulses of safety, in comparison to the other sites. Wolves were more patchily distributed and intermittently present on the Gallatin Canyon (GC) site, so in comparison to NR, GC elk experienced more continuous safety with pulses of risk. Elk in the Elkhorn Mountains (EH) were not exposed to wolves during this study. Figure 2 shows the temporal sequence of wolf presence and absence in one drainage of the Gallatin Canyon, as a representative example of temporal variation in periods of safety (wolf absence) and risk (wolf presence).

Table 1 summarizes the predicted patterns of antipredator responses across these sites for the three hypotheses. The prediction of the risky times model is that vigilance will be greater when wolves are immediately present than when they are immediately absent (Y > N), but within periods of wolf presence or wolf absence, this model does not directly predict differences among sites. The prediction of the risky places model is that sites with greater long-term risk will provoke greater vigilance (Northern Range > Gallatin Canyon > Elkhorn Mountains), but this model makes no direct predictions about the response of vigilance to temporal variation in wolf presence within sites. The specific predictions of the risk allocation model are best understood by reference to Fig. 1. Only the risk allocation model directly predicts that vigilance should respond to an interaction between long-term differences in risk among sites and short-term temporal variation in risk within sites, so that all five combinations of sites and wolf presence/absence are explicitly predicted to yield different levels of vigilance.

METHODS

We observed elk under known conditions of risk on three sites within the Greater Yellowstone region. Over 4 winters, we made observations between December and May, when elk aggregate at relatively low elevations and are more easily observed. Winter starvation is an important limiting factor for elk in this ecosystem (Delguidice et al. 1991; Singer et al. 1998; Garrott et al. 2003), and fitness trade-offs between vigilance and foraging are likely to be strongest in winter, when forage quality is low and access is restricted by snow. We have previously shown that vigilance levels increase on days that wolves are locally present, and the proportion of time spent foraging decreases (Winnie & Creel 2007).

Study Areas

The three study sites were all centred on river valleys typified by open grassy meadows or sagebrush at low elevation and coniferous woodlands on the slopes above. The sites experience comparable weather, though there is less snow accumulation on the Elkhorn site. Elk are the most abundant ungulate on all three study areas, and elk are the primary prey of wolves throughout the region. For the Gallatin Canyon and Northern Range sites, wolves are the primary predator of adult elk, accounting for approximately 90% of the predation on adults (Smith et al. 2004; Creel & Winnie 2005; Stahler et al. 2006; Winnie & Creel 2007). Mountain lions, *Puma concolor*, take elk on all three sites at unknown but relatively low rates. Grizzly bears, *Ursus arctos*, prey on newborn elk in the early summer on the Gallatin Canyon and Northern Range sites, but very rarely prey on adult elk and are in hibernation during the winter months when we conducted our field work. Human hunting is allowed on the Gallatin Canyon site, but relatively few elk were on the site during the fall general hunting season during the years of this study. A mean of 80 licenses has typically been issued for a late-season hunt (closed during this study), with a long-term average of 63% success.

Gallatin Canyon

The GC site lies in the west of the Greater Yellowstone Ecosystem and holds one of seven native Montana elk herds (Hamlin 2004). The site covers 125.8 km^2 in four drainages (Porcupine, Taylor, Tepee and Daly) that hold most of the Gallatin elk herd in winter. During the observations for this study, 5 to 17 wolves in two or three packs occupied the study area. The Gallatin winter elk herd has numbered 1214–3028 elk since 1927, holding relatively

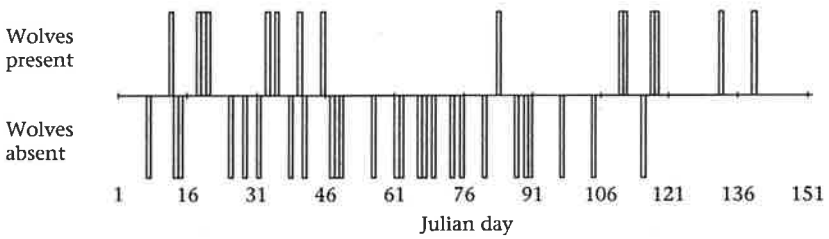


Figure 2. The temporal sequence of wolf presence and absence in one drainage of the Gallatin Canyon over one study season, as a representative example of the temporal distribution of immediate safety and risk in a wild population of elk. The Gallatin site comprised four such drainages. Gallatin elk typically experience pulses of risk (above) against a background of more continuous safety (below). On days with no bar, we did not determine wolf presence/absence for this drainage.

Author's personal copy

Table 1. A summary of predicted patterns of vigilance under alternative hypotheses about the antipredator response rules of elk

Model	Predicted strength of antipredator responses
Risk allocation	GC/Y>NR/Y>EH/N>GC/N>NR/N
Risky times	NR/Y=GC/Y>NR/N=GC/N>EH/N
Risky places	NR/Y=NR/N>GC/Y=GC/N>EH/N
Null	EH=GC/Y=GC/N=NR/Y=NR/N

The two-letter code denotes sites: GC: Gallatin Canyon; NR: Northern Range; EH: Elkhorn Mountains. The one-letter code denotes wolf presence (Y) or absence (N) within a 3.2-km radius on the day of observation.

stable around the long-term average of 1653 animals. A significant decline in population size over time has been driven primarily by low counts in the years since recolonization by wolves (Creel et al. 2005; Creel & Christianson 2008). Valley bottoms are primarily sage (*Artemesia*) scrub and grassland (predominantly Idaho fescue and bluebunch wheatgrass: *Festuca idahoensis* and *Agropyron spicatum*) with small riparian zones and coniferous forest and small meadows on the slopes above. Elk comprise >90% of the Gallatin ungulate community, usually in small herds (mean $\pm$ SE = 13.9 $\pm$ 0.67 elk, max = 253). Relatively few elk occupy the steep, rocky terrain between the four focal drainages. Conventional VHF radiotelemetry and GPS telemetry (Creel et al. 2005) show that elk move between the four drainages, but rarely during our field season. Moose, *Alces alces*; mule deer, *Odocoileus hemionus*; and white-tailed deer, *Odocoileus virginianus*, also used the Gallatin site, at densities much lower than elk (3.3% of 2846 herds).

Northern Range

The 830-km^2 Northern Range site lies in the northeast portion of Yellowstone National Park, in an area defined by the seasonal migration of a large elk herd that occupies the area. Wolf numbers on the site varied from 84 wolves in seven packs in 2005 to 54 wolves in six packs in 2006. The study area is dominated by large open valleys comprising sage (*Artemesia* spp.) and grassland (*Festuca* and *Agropyron* spp.) with riparian areas bordering the small creeks and the Yellowstone, Lamar and Gardner rivers. The upper elevations and north-facing slopes are primarily coniferous forests (*Pinus* and *Pseudotsuga* spp.) with small interspersed meadows. Elk, previously numbering 16 000 to 19 000 animals but recently numbering 6000–8000, are the most numerous ungulate on the site (Smith et al. 2004), followed by bison (*Bison bison*), numbering 600–700 animals (Smith et al. 2004). Moose, mule deer, white-tailed deer and bighorn sheep, *Ovis canadensis*, occur at low densities.

Elkhorn Mountains

The risk allocation model predicts that vigilance during a brief pulse of safety will be lower than vigilance during continuous safety (Lima & Bednekoff 1999). To obtain a small sample of baseline data on the vigilance levels of elk that were continuously safe from wolf predation, we observed elk in the Elkhorn Mountains during 19 sampling periods on 8 widely separated days in the winters of 2005 and 2006. The Elkhorn Mountains are a small, isolated mountain chain at the northwestern edge of the Greater Yellowstone Ecosystem. At the time of this study the site had no reports of wolf presence for more than 70 years. Grizzly bears were not known to occupy the site, but human hunting occurred in the fall and mountain lions were present. Like the other two sites, the Elkhorn site is dominated by large open valleys comprising sage and grassland with riparian areas bordering watercourses, and the upper elevations and north-facing slopes are primarily coniferous forests with small interspersed meadows. Elk densities were qualitatively comparable to those of the other sites during our observations.

Behavioural Observations

Following published methods (Winnie & Creel 2007; Liley & Creel 2008) we used scan sampling to record elk behaviour using six categories: feeding, moving, bedded, standing vigilant, bedded vigilant, and other. For the analyses reported here we determined total vigilance, the sum of standing vigilance and bedded vigilance. We scored an elk as vigilant, whether standing or laying down, if it held its head at approximately a right angle above its back, with a steady gaze and ears focused forward in the direction of the gaze. Elk scored as vigilant while bedded were always resting upright on their sternums; laterally recumbent elk were never vigilant. Postures adopted by elk when they are vigilant by these criteria are easily recognized, and interobserver reliability was >95%. All results we report for total vigilance were confirmed by analyses restricted to standing vigilance.

We determined the proportion of elk that were vigilant in 3126 instantaneous scan samples, conducted at 5-min intervals in 426 separate observation periods, with a mean of 7.4 scans per observation. Herd size averaged 11.2 $\pm$ 0.8 (SE) elk for the herds observed in this sample, and we recorded a total of 35 605 behaviour determinations on 4771 individual elk, between 2003 and 2006. To avoid pseudoreplication, we collapsed these observations into a single proportion vigilant for each observation period, taking the mean across individuals and scans. We recorded the size and composition of each herd, because these variables have been shown to affect the vigilance of elk (Childress & Lung 2003; Winnie & Creel 2007; Liley & Creel 2008).

We scored wolves as locally present or absent on the day of observation for 651 days, using methods previously described for the Gallatin site (Creel et al. 2005) and for the Northern Range site (Liley & Creel 2008). Briefly, we recorded wolves as locally present if we detected them by any combination of direct sighting, VHF telemetry, howls, fresh scats or tracks (in snow or loose soil and mud) or a fresh wolf kill. We determined wolf presence/absence at the scale of single drainages in the Gallatin Canyon, which on average had an area equal to a circle with

Author's personal copy

a radius of 3.2 km (see Creel et al. 2005 for map). To obtain comparable data from the Northern Range, we first located wolves by VHF telemetry and then used a GPS to determine the linear distance to the elk herd that we observed, scoring wolves as present if the distance was less than 3.2 km and taking care to check for other wolves in the area (for further details see Liley & Creel 2008). These methods have substantial power to detect the effects of wolf presence on elk behaviour (Winnie & Creel 2007), grouping patterns (Creel & Winnie 2005; Winnie & Creel 2007), habitat selection (Creel et al. 2005), sensitivity to environmental conditions (Winnie et al. 2006) and reproductive physiology and demography (Creel et al. 2007).

With the proportion of time spent vigilant as the dependent variable, we used maximum likelihood to fit a general linear model (GLM) controlling the effects of herd size and composition while testing for differences among sites (spatial responses), differences in the immediate presence or absence of wolves (temporal responses) and interaction between these two effects. We used the Wald statistic to test individual effects within this GLM. Finally, we confirmed that none of the reported inferences changed when we fit a more complex GLM that included all of the above variables, plus snow cover and the distance to protective cover. Because we have examined these effects elsewhere, we do not discuss unnecessarily complex models any further here. To meet the model's assumptions, we logit transformed the proportion of time spent vigilant prior to analysis and confirmed that the transformation was appropriate by examining the distribution of residuals. In the text we report raw means with standard errors. In Fig. 3 we show back-transformed least-squares means and 95% confidence intervals from GLM, with continuous covariates fixed at their means.

To accommodate those who believe that this analysis should use a model-selection approach rather than hypothesis testing, we used Akaike's information criterion (AIC) to compare a set of GLMs that included or excluded responses of vigilance to spatial and temporal variation in wolf presence. Before analysing the data, we identified a small set of models (Table 2) that (1) varied in complexity, (2) encapsulated the hypotheses that vigilance might vary among places, times or both and (3) included or excluded covariates such as herd size and composition. The inferences reached are the same with either approach.

This research was conducted with IACUC approval from Montana State University (Protocol 40-07).

RESULTS

Wolves were present on 67.6% of 324 days on the NR site and 39.8% of 319 days on the GC site. Wolves were absent from the EH site, where we observed elk on 19 occasions over 8 days to give an estimate of baseline vigilance levels in a local population without wolves.

Vigilance decreased as herd size increased (Wald test: $W_1 = 13.5$, $P < 0.001$). Vigilance was not detectably affected by herd composition ($W_1 = 1.30$, $P = 0.254$) after controlling for the other effects: this result is at least partially due to colinearity between herd size and composition, because larger herds consistently hold a higher proportion of females (Winnie & Creel 2007; Liley & Creel 2008).

Elk were significantly more vigilant (Wald test: $W_1 = 24.6$, $P < 0.001$) when wolves were present (vigilance: $\overline{X} \pm \text{SE} = 7.3 \pm 0.1\%$) than when wolves were absent (vigilance: $3.6 \pm 0.1\%$). This effect matches the primary prediction of the risky times hypothesis, but also matches the risk allocation hypothesis. The proportion of time that elk were vigilant varied across sites by a factor of 4 ($W_2 = 30.3$, $P < 0.001$), from $2.7 \pm 0.2\%$ on the EH site to $4.8 \pm 0.1\%$ on the NR site and $10.9 \pm 0.1\%$ on the GC site. Overall, GC elk were more than twice as vigilant as NR elk, even though GC elk were exposed to wolves only 59% as often as NR elk. This variation among sites directly opposes the primary prediction of the risky places hypothesis and is not predicted by the risky times hypothesis.

Perhaps counterintuitively, the pattern that GC elk were more vigilant than NR elk is directly predicted by the risk allocation hypothesis (Fig. 1; Lima & Bednekoff 1999). Also as predicted by the risk allocation hypothesis (Fig. 1), GC elk were more vigilant than NR elk with wolves present and with wolves absent (Fig. 3). Finally, as predicted by the risk allocation hypothesis (Fig. 1), vigilance responded to the immediate presence of wolves more strongly on the NR site than on the GC site (Fig. 3; site × wolf presence interaction: $W_1 = 5.51$, $P = 0.019$). Contrary to the details of the risk allocation hypothesis (Fig. 1), vigilance levels of NR and GC elk when wolves were absent were not lower than those of EH elk, and vigilance levels were higher for GC elk than for EH elk (Fig. 3).

Using AIC scores to compare a set of a priori models of vigilance (Table 2), we found that the two models with

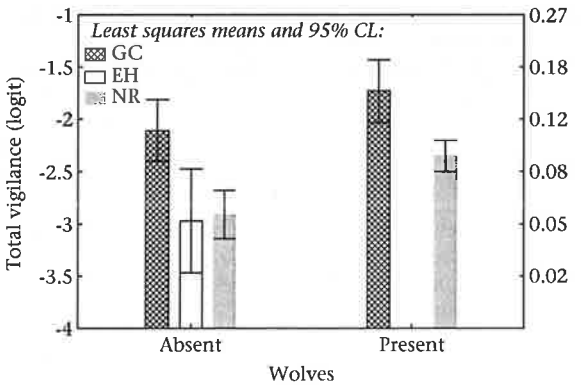


Figure 3. The proportion of time that elk were vigilant in the immediate presence or absence of wolves on that day, for three sites that differed in background levels of risk. See Fig. 1 for predicted levels of vigilance under the risk allocation model and Table 1 for predictions from each of the general models of vigilance. Bars show least-squares means with continuous covariates fixed at their mean values, and whiskers show 95% confidence intervals for logit-transformed data. The right axis is back-transformed to the proportion of time spent vigilant: note that this yields nonadditive scaling.

Author's personal copy

Table 2. An a priori set of general linear models of vigilance by elk compared using Akaike's information criterion (AIC)

Model	*df*	ΔAIC
Site*, wolf†, site×wolf, herd size	5	0
Site, wolf, site×wolf, herd composition‡, herd size	6	0.7
Site, wolf, herd size	4	3.0
Site, wolf	3	9.2
Site, wolf, site×wolf	4	9.9
Site, site×wolf	3	26.6
Site	2	27.2
Wolf, site×wolf	2	31.2
Wolf	1	31.3
Herd size	1	39.5
Herd size, herd composition	2	41.3

For the best model, AIC = 914.3 and deviance/*df* = 1.022.
*Differences among Northern Range, Gallatin and Elkhorn sites, i.e. spatial variation in risk.
†Differences between days with wolves present or absent, i.e. temporal variation in risk.
‡Proportion of the herd comprising adult females, who are more vigilant than males.

good support from the data (ΔAIC < 2.0) included temporal variation in risk, spatial variation in risk and spatiotemporal interaction, as predicted by risk allocation but not by the risky times or risky places hypotheses.

DISCUSSION

Overall, the data gave strong support to risk allocation, equivocal support to the risky times hypothesis, and no support to the risky places hypothesis. Contrary to risky places but as predicted by risk allocation, Gallatin elk were more vigilant than Northern Range elk, both when wolves were present and when they were absent, despite lower exposure to risk than in the Northern Range. This result, and the broader recognition that the risk allocation and risky places hypotheses make contradictory predictions, has important ramifications for studies of the ecological consequences of predator loss or reintroduction. Most studies make the assumption that *all* of the ecological consequences of predation are stronger in places with more frequent exposure to risk, an assumption that is eminently reasonable at first glance. The risk allocation hypothesis (supported by our data on elk vigilance) suggests that the costs of vigilance could counterintuitively show an inverse relationship to the frequency of exposure to predators. If these results prove to be general, research approaches that consider only spatial variation in risk could have limited utility for questions about behaviourally mediated effects of predation.

Like the risk allocation hypothesis, habituation can potentially explain weaker antipredator responses with more frequent exposure to risk. This is an important consideration for study designs that expose prey to cues of predator presence, but do not expose them to any genuine risk. In studies that observe responses to true predation risk, habituation to genuinely lethal predators seems unlikely. For elk in this ecosystem, wolf predation is common, with important effects on elk population dynamics (Smith et al. 2004; White & Garrott 2005; Creel & Christianson 2008).

We have previously shown that progesterone levels of females and calf production were lower at sites with high predator–prey ratios, in a comparison of elk on several winter ranges (Creel et al. 2007). In that analysis, we did not directly consider the temporal pattern of risk; nonetheless, risk effects on prey demography were stronger at risky sites, contrary to the pattern reported here for vigilance levels. Other studies have also shown that wolf predation affected prey dynamics more strongly in places with more frequent exposure to risk, though these studies do not distinguish between direct predation and behaviourally mediated risk effects (Hebblewhite et al. 2002, 2005). This juxtaposition of results highlights the need for field studies that measure the total impact of predation, via direct killing and via behaviourally mediated risk effects (Brown et al. 1999; Preisser et al. 2005; Pangle et al. 2007). These results also highlight the fact that prey can use many different behavioural responses to risk, and these behavioural responses may be additive or compensatory in their effects on prey demography and dynamics (Lind & Cresswell 2005). Elk respond to wolves by altering their time budgets (Childress & Lung 2003; Fortin et al. 2004; Winnie & Creel 2007), habitat selection (Fortin et al. 2005; Creel et al. 2005; Hernandez & Laundre 2005), grouping patterns (Hebblewhite & Pletscher 2002; Creel & Winnie 2005), sensitivity to environmental conditions (Winnie et al. 2006) and diet (Hernandez & Laundre 2005; Christianson & Creel, in press). At present, we do not know how each of these responses is affected by the temporal sequence into which pulses of risk and safety are imbedded. Finally, one 'unit' of vigilance does not necessarily have the same impact on fitness under all circumstances (Illius & FitzGibbon 1994; Fortin et al. 2004).

When considering the predictions of the risk allocation hypothesis (as originally laid out by Lima & Bednekoff 1999; see Fig. 1), one must recall that Northern Range elk are most often in the high-risk condition (upper line, Fig. 1), whereas Gallatin Canyon elk are most often in the low-risk condition (lower line, Fig. 1). Depending on the quantitative manner in which optimal vigilance declines as the frequency of predator exposure increases, it is possible that Gallatin elk would be predicted to be more vigilant than Northern Range in both the high-risk and the low-risk conditions, but still predicted to be less vigilant overall, once each prediction is weighted by the proportion of time to which it pertains. To our knowledge, no species has yet been studied in a manner that would allow the details of the curves in Fig. 1 to be described quantitatively.

In summary, patterns of vigilance by elk support the risk allocation hypothesis and directly oppose the risky places hypothesis. Tests in the wild with other species and ecosystems to assess the generality of this result are a high priority, because most assessments of the ecological impacts of predators implicitly assume that the effects of predation increase with increasing frequency

Author's personal copy

of exposure to risk. Direct killing rates should have a positive correlation with the frequency with which predators use a site, but the costs of antipredator behaviour (risk effects) could show an inverse relationship (as has been shown in a different manner by Creel & Christianson 2008). This conclusion reinforces the need for empirical studies of the relative magnitudes of direct effects and risk effects in determining the total effect of predators on prey dynamics. Such studies will improve our understanding of the consequences of predator losses and reintroductions, both for prey and for the species with which prey interact (Shurin et al. 2002; Werner & Peacor 2003).

Acknowledgments

We thank Doug Smith for his cooperation in field work on the Northern Range, Montana Fish, Wildlife and Parks and Yellowstone National Park for permission to conduct the research, and the staff of the Yellowstone Center for Resources for their assistance. This study was supported by a grant from the National Science Foundation's Animal Behavior Program. Our thanks to Peter Bednekoff, Ted Stankowich and Dan Blumstein for their careful and useful reviews.

References

Brown, J. S., Laundre, J. W. & Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385–399.

Childress, M. J. & Lung, M. A. 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, **66**, 389–398.

Christianson, D. & Creel, S. In press. Risk effects in elk: sex-specific response in grazing and browsing due to predation risk from wolves. *Behavioral Ecology*.

Creel, S. & Christianson, D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, **23**, 194–201.

Creel, S. & Winnie, J. A. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, **69**, 1181–1189.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. L. & Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.

Creel, S., Christianson, D., Liley, S. & Winnie, J. A. 2007. Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960.

Delguidice, G. D., Singer, F. J. & Seal, U. S. 1991. Physiological assessment of winter nutritional deprivation in elk of Yellowstone National Park. *Journal of Wildlife Management*, **55**, 653–664.

Fortin, D., Boyce, M. S., Merrill, E. H. & Fryxell, J. M. 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos*, **107**, 172–180.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. & Mao, J. S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Frid, A., Baker, G. & Dill, M. 2008. Do shark declines create fear-released systems? *Oikos*, **117**, 191–201.

Garrott, R. A., Eberhardt, L. L., White, P. J. & Rotella, J. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology–Revue Canadienne de Zoologie*, **81**, 33–45.

Griffin, P. C., Griffin, S. C., Waroquiers, C. & Mills, L. S. 2005. Mortality by moonlight: predation risk and the snowshoe hare. *Behavioral Ecology*, **16**, 938–944.

Hamilton, I. M. & Heithaus, M. R. 2001. The effects of temporal variation in predation risk on anti-predator behaviour: an empirical test using marine snails. *Proceedings: Biological Sciences*, **268**, 2585–2588.

Hamlin, K. L. 2004. *Montana Elk Management Plan*. Helena, Montana: Montana Fish, Wildlife & Parks.

Hebblewhite, M. & Pletscher, D. H. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology–Revue Canadienne de Zoologie*, **80**, 800–809.

Hebblewhite, M., Pletscher, D. & Paquet, P. C. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology–Revue Canadienne de Zoologie*, **80**, 789–799.

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E. & Paquet, P. C. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**, 2135–2144.

Hernandez, L. & Laundre, J. W. 2005. Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, **11**, 215–220.

Illius, A. W. & FitzGibbon, C. 1994. Costs of vigilance in foraging ungulates. *Animal Behaviour*, **47**, 481–484.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. & Boyce, M. S. 2007. Landscape heterogeneity shapes predation in a newly restored predator prey system. *Ecology Letters*, **10**, 690–700.

Kruuk, H. 2002. *Hunter and Hunted: Relationships between Carnivores and People*. Cambridge, U.K.: Cambridge University Press.

Liley, S. & Creel, S. 2008. What best explains vigilance in elk: characteristics of prey, predators, or the environment? *Behavioral Ecology*, **19**, 245–254.

Lima, S. L. 1990. Protective cover and the use of space: different strategies in finches. *Oikos*, **58**, 151.

Lima, S. L. & Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist*, **153**, 649–659.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lind, J. & Cresswell, W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945–956.

Mitchell, W. A. & Lima, S. L. 2002. Predator–prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos*, **99**, 249–259.

Pangle, K. L., Peacor, S. D. & Johannsson, O. E. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology*, **88**, 402–412.

Pecor, K. W. & Hazlett, B. A. 2003. Frequency of encounter with risk and the tradeoff between pursuit and antipredator behaviors in crayfish: a test of the risk allocation hypothesis. *Ethology*, **109**, 97–106.

Preisser, E. L., Bolnick, D. I. & Blumstein, D. T. 2005. Scared to death? The effects of intimidation and consumption in predator prey interactions. *Ecology*, **86**, 501–509.

Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D. & Halpern, B. S. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785–791.

Author's personal copy

Sih, A. & McCarthy, T. M. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour*, **63**, 437–443.

Singer, F. J., Swift, D. M., Coughenour, M. B. & Varley, J. D. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968–1993. *Wildlife Society Bulletin*, **26**, 375–390.

Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S. & Evans, S. B. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management*, **68**, 153–166.

Stahler, D. R., Smith, D. W. & Guernsey, D. S. 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. *Journal of Nutrition. Supplement*, **136**, 1923S–1926S.

Sundell, J., Dudek, D., Klemme, I., Koivisto, E., Pusenius, J. & Ylonen, H. 2004. Variation in predation risk and vole feeding behaviour: a field test of the risk allocation hypothesis. *Oecologia*, **139**, 157–162.

Van Buskirk, J., Mnller, C., Portmann, A. & Surbeck, M. 2002. A test of the risk allocation hypothesis: tadpole responses to temporal change in predation risk. *Behavioral Ecology*, **13**, 526–530.

Werner, E. E. & Peacor, S. D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.

Werner, E. E., Gilliam, J. F., Hall, D. J. & Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.

White, P. J. & Garrott, R. A. 2005. Yellowstone's ungulates after wolves: expectations, realizations, and predictions. *Biological Conservation*, **125**, 141–152.

Winnie, J. & Creel, S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, **73**, 215–225.

Winnie, J., Christianson, D., Creel, S. & Maxwell, B. 2006. Elk decision-making rules are simplified in the presence of wolves. *Behavioral Ecology and Sociobiology*, **61**, 277–289.

Wolff, J. O. & Van Horn, T. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology–Revue Canadienne de Zoologie*, **81**, 266–271.