Behaviour of spruce grouse broods in the field

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Behaviour of juvenile spruce grouse (*Dendragapus canadensis*), from hatching to brood breakup, was observed in 30 radio-tracked broods inhabiting lodgepole pine (*Pinus contorta*) forests of southwestern Alberta. The immediate posthatch period (first 20 days) was characterized by a close spatial relationship between the chicks and hen, with brooding being the dominant behaviour. Hens with broods appeared to respond immediately, both vocally and through movement toward their chicks, whenever the latter uttered the following calls: sreep, sury, seer, and purring. Brooding sessions decreased in frequency but not duration (median of 11 min) until they disappeared from the behavioural repertoire of the chicks at about 50 days of age. Hen–chick and intersibling distances increased as the chicks grew older. The breakup of broods appeared to result when the cohesiveness of the brood decreased to a point at which calls of the chicks no longer elicited a response from the brood hen. There was no evidence that agonism contributed to this decline in brood cohesion.

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Le comportement de tétras des savanes (*Dendragapus canadensis*) a été observé de l'éclosion à la dispersion des portées chez 30 portées suivies par radio dans les forêts de pins (*Pinus contorta*) du sud-ouest de l'Alberta. La période qui suit immédiatement l'éclosion (les 20 premiers jours) se caractérise par une étroite relation spatiale entre les oisillons et leur mère et l'incubation constitue le comportement dominant. Les poules couveuses semblent réagir immédiatement, soit vocalement, soit par des mouvements vers les petits, lorsque les oisillons utilisent des cris tels que "srîp", "surré" ou "sîr" ou des ronronnements. Les sessions de couvaison diminuent de fréquence, mais pas de durée (médiane de 11 minutes) jusqu'à disparaître du répertoire de comportements lorsque les oisillons atteignent environ 50 jours. Les distances mère–oisillons et oisillons–oisillons augmentent à mesure que vieillissent les petits. La dispersion des portées semble se produire lorsque les liens entre les oisillons diminuent au point où les cris des oisillons ne provoquent plus de réactions chez la mère. La diminution des liens au sein de la portée ne semble pas due à de l'antagonisme.

[Traduit par le journal]

Introduction

The spruce grouse, *Dendragapus canadensis*, is a widespread species of the Tetraoninae found in the boreal forests of North America. Previous research has shown the importance of the behaviour of adult spruce grouse in understanding such population attributes as dispersion and territoriality (Ellison 1971; Herzog and Boag 1978; Nugent and Boag 1982). Although the behaviour of juveniles has frequently been suggested to be important in determining their subsequent behavioural patterns as adults (Herzog and Boag 1978; Alway and Boag 1979; Boag *et al.* 1979; Keppie 1979; Herzog and Keppie 1980; Schroeder 1985*b*), detailed examination of juvenile spruce grouse behaviour, especially while still in broods, has been limited to captive situations (Alway 1977; Alway and Boag 1979).

The purpose of this study was to examine under field conditions the behaviour of juvenile spruce grouse while in broods. By observing broods repeatedly over time, it was possible to describe the ontogeny of behaviour in the field and to compare it with that recorded in captivity. Furthermore, the use of radio telemetry made it possible to find at will broods in the wild and to observe these relatively undisturbed birds under a variety of conditions in both space and time.

Methods

The behaviour of spruce grouse broods was studied from 1982 to 1984 near the R. B. Miller Biological Station (50°39′ N, 114°39′ W), 27 km west of Turner Valley, Alberta. The study area consisted of about 10 000 ha of forest dominated by lodgepole pine (*Pinus contorta*), with scattered clumps of white spruce (*Picea glauca*), poplar (*Populus* spp.), and alpine fir (*Abies lasiocarpa*).

All grouse used in this study were individually marked with a unique combination of coloured leg bands after being noosed (Zwickel and Bendell 1967). To assure access to broods immediately after they hatched, 23 females were harnessed with radio transmitters before incubation began in early June. Nine of these females subsequently produced broods and were observed regularly after being found with the aid of radio telemetry. Radios were also attached to 21 additional hens found with chicks, thus increasing the total sample size to 30 broods. Hatch dates for all broods were determined to the nearest day from estimated ages of the chicks based on measured lengths of two primaries (McCourt and Keppie 1975).

Broods were observed for varying lengths of time over the entire daylight period (0500 to 2230) for a total of about 300 hours. After a brood was initially located, an attempt was made to follow and observe it from a distance of 10–20 m. Although observation sessions lasted as long as 10 h, they were terminated if the brood was obviously disturbed by the presence of the observer. A small percentage of brood hens (10%) was essentially impossible to follow without causing disturbance. The rest of the sample (27) apparently ignored us and appeared to behave normally, often moving and (or) feeding within 1 m of the observer.

During each period of observation, scans (Altmann 1974) of the birds were taken every 8 min. During each scan, which took a maximum of 15 s to complete, the spatial dispersion, behaviour (Table 1), and vocalizations (Table 2) of each visible member of the brood and the hen were recorded. All observed occurrences of every behaviour except feeding, being alert, and loafing and every vocalization except sreep, heep, sury, and seer were recorded. In addition to the normal scans, the location of the brood was noted every 16 min and plotted on a map of the study area using a grid system superimposed over air photos.

Because of the nonnormality of the data sets, all values of distance and time for a given age are given as medians rather than means. Regression analysis was used in comparing space and time parameters against age of chicks.

Results

Brooding behaviour

The first phase (20 days) in the posthatch life of the brood

TABLE 1. Behavioural repertoire of spruce grouse recorded in radio-tracked broods in southwestern Alberta

Behaviour	Origin of previous descriptions					
	Lumsden 1961	MacDonald 1968	Harju 1969	Hjorth 1970	Alway 1977	Alway and Boag 1979
Foraging			Feeding		Feeding	
Brooding			Brooding		Brooding	
Loafing						
Preening						
Dust-bathing						
Flapping-run					Flap-run	Flapping-run
Alert			Alert		Alert	
Erect					Erect	
Aggressive		Aggressive	Aggressive		Aggressive	
Upright				Upright	Upright	
Jerky-crouch					Nervous-crouch	Jerky-crouch
Crouching with head-shaking	Head-jerk display	Squatting display		Crouching-cum-head-shaking	Crouching-cum-head-shaking	
Display-walk with tail-swaying	Strutting display	Tail-swishing display	Strutting display	Display-walk-cum-tail-swaying	Display-walk-cum-tail-swaying	
Rush with momentary tail-fanning	Tail-flick display	Tail-swishing display	Tail-flick display	Rush-cum-momentary-tail-fanning	Rush-cum-momentary-tail-fanning	

was characterized by the juvenile's dependence on brooding behaviour of the hen. Juveniles appeared to initiate brooding bouts by uttering sury calls which, to the human ear, were a more insistent form of the sreep calls, apparently given as the chicks became chilled. On three separate occasions, juveniles that were being held temporarily in a darkened container in the field pending measurement began giving the sury call. These calls apparently stimulated the uncaptured hen to approach the container holding the chicks and to assume a brooding posture (a semicrouched position in which the feathers of the ventral pterylae are erected) beside it.

In undisturbed situations, the brood hen appeared to respond to sury calls of the chicks by first selecting an appropriate spot to brood the chick(s) before assuming a brooding posture. Occasionally the hen would stand up and select a second spot immediately after the initial assumption of a brooding posture. The chicks followed the hen closely during this period of site selection and attempted to move under the hen while giving the sury call. After the hen selected a brooding spot and assumed a brooding posture, most chicks approached from the front and pushed their way underneath. While brooding, the hen typically uttered heep calls. Brooding bouts may have been terminated by vocal stimuli from the chicks, as they were frequently heard giving both sury and sreep calls while being brooded. Sreep calls were noticeably more frequent immediately preceding the end of the brooding bout. It is possible that the hen stopped brooding the chicks when their sury calls ceased, perhaps indicating that the chicks were no longer cold. On occasion, individual chicks would move out from beneath the brood hen before she stood up, a situation very similar to that observed in wild blue grouse (*Dendragapus obscurus*) (Zwickel 1967).

The duration of undisturbed brooding bouts varied around a median of 11 min regardless of the age of the chicks (Fig. 1). Although no relationship between chick age and duration of brooding bout was evident, more brooding bouts of older chicks (>20 days old) than those of younger chicks (≤20 days old) appeared to be in response to cool temperatures (≤10°C) ($P < 0.001$; χ^2 contingency table).

TABLE 2. Spruce grouse vocalizations recorded from brood hens and their chicks under field conditions in southwestern Alberta

Vocalization	Origin of previous descriptions		
	Harju 1969	Alway 1977	Nugent and Boag 1982
Sreep		Contact[a]	
Heep	Brooding[a]	Contact[a]	
Purring	Contentment[a]	Pleasure[a]	
Sury		Brooding	
Seer	Distress[a]	Distress[a]	
Cantus	Aggressive[a] Alarm[b]	Aggressive[a]	Cantus[a]
Hum	Warning	Warning[a]	
Alarm		Alarm[a]	
Gull		Gull	

[a] The original description includes a sonogram.
[b] The sonogram and the behavioural context in which it was recorded suggest that this alarm call is actually part of the cantus.

Brooding behaviour was observed with decreasing frequency until it disappeared from the behavioural repertoire at about 50 days of age (Fig. 2). Observations of undisturbed broods over long periods of time (more than 3 h) showed that brooding bouts at all ages tended to decrease in frequency, if not duration, as temperatures rose from relatively cool levels in the morning to warmer levels later in the day (Fig. 3). Broods observed for short periods indicated similar trends. Notable exceptions occurred on cloudy, rainy, and (or) cold days (Fig. 3; broods of 15, 17, 18, 28, and 50 days of age). The late brooding bouts observed in a brood of 50-day-old chicks occurred when the temperature was 0°C. The two chicks, which were about 62% the size of the hen, forced their way beneath the brooding hen, apparently causing her to loose her footing and fall off the chicks. Presumably no more than two chicks of this age could be brooded because of their large size. By contrast, the earliest a brood was observed roosting in trees at night (a time of day when they would be most likely to brood) was at 33 days of age. These results suggest that

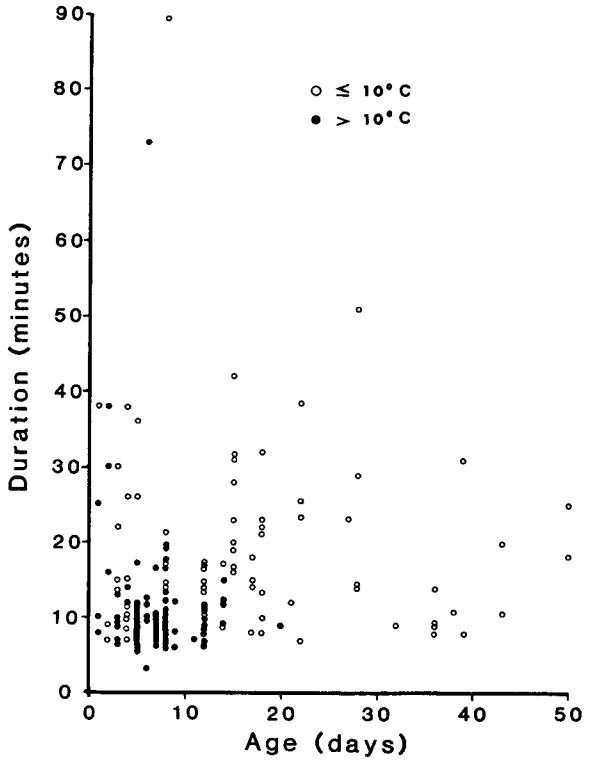

FIG. 1. Length of brooding bouts (n = 161) by age and temperature for spruce grouse in southwestern Alberta (r^2 = 0.01; P = 0.203).

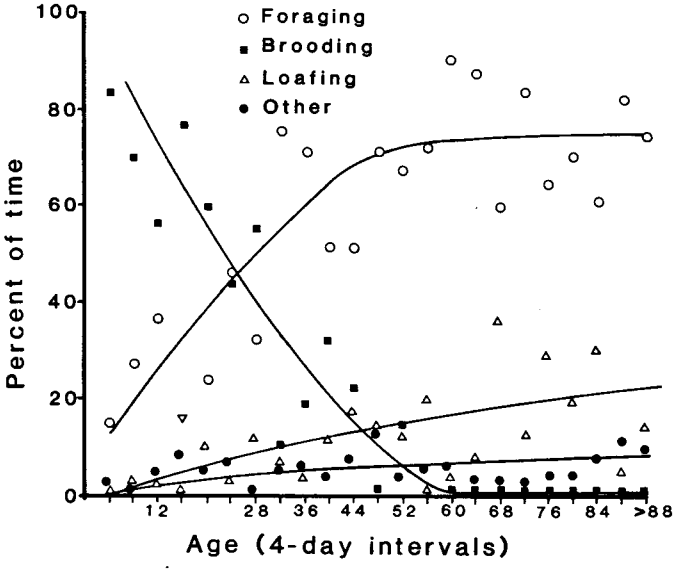

FIG. 2. Time budget for feeding, brooding, loafing, and other activities (sexual displays and agonistic interactions) of spruce grouse broods in southwestern Alberta. Points represent 4-day age categories and include a minimum of 3 h observation time (23 scans) divided equally among at least three different broods. Lines fitted to points by eye.

brooding frequency is influenced by both ambient conditions (temperature and precipitation) and the thermoregulatory capacity of chicks (a function of age).

Foraging behaviour

As broods grew older, they spent less time being brooded and more time foraging (Fig. 2). The amount of foraging time

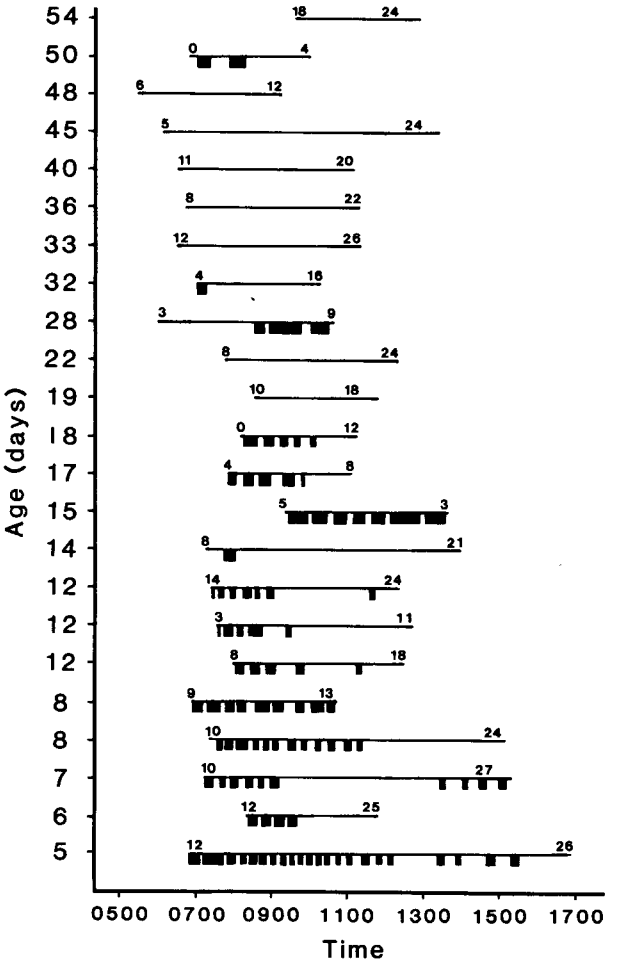

FIG. 3. Periods of more than 3 h during which broods of spruce grouse were observed undisturbed in southwestern Alberta. Numbers above lines indicate the temperature (degrees Celsius) at the onset and termination of observation period. Black bars beneath the lines indicate duration of brooding bouts.

stabilized at about 75% of the daylight hours when the chicks reached 50 days of age. The other 25% of the time consisted of loafing and other behaviours such as agonistic interactions and displays. As suggested by Zwickel (1967) for blue grouse, spruce grouse chicks are apparently not shown what to eat; the brood hen often fed on foods out of reach of the chicks. However, since the general foraging areas were determined by the hen, she may have indirectly governed what they fed upon.

Contact among brood members while foraging seemed to be maintained with the sreep calls of juveniles, to which the brood hen responded with heep calls. Sreep calls were uttered while chicks were foraging relatively close to the hen. The sreep calls of chicks and the heep calls of hens differed in sound and apparently in function. Sreep calls were much higher in pitch than heep calls which they elicited from brood hens. Adult females also uttered "chicklike" sreep calls in the fall, winter, and early spring when in flocks with other spruce grouse, presumably in a contact-call situation.

The typical dispersion patterns of feeding juveniles placed them at increasing distances from their brood hen with increasing age (Fig. 4). There was no difference between juvenile males and females (P = 0.183; ANCOVA) in this attribute. When the chicks lost contact (visual and (or) auditory) with the brood hen, they gave seer calls. Seer calls typically initiated a

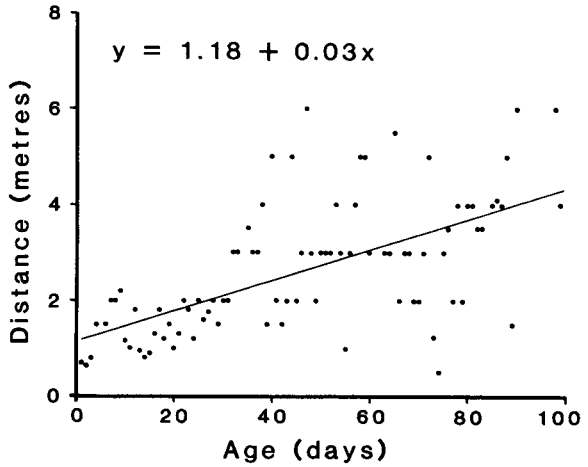

FIG. 4. Median distances between spruce grouse brood hens and their foraging chicks of various ages ($r^2 = 0.38$; $P < 0.001$).

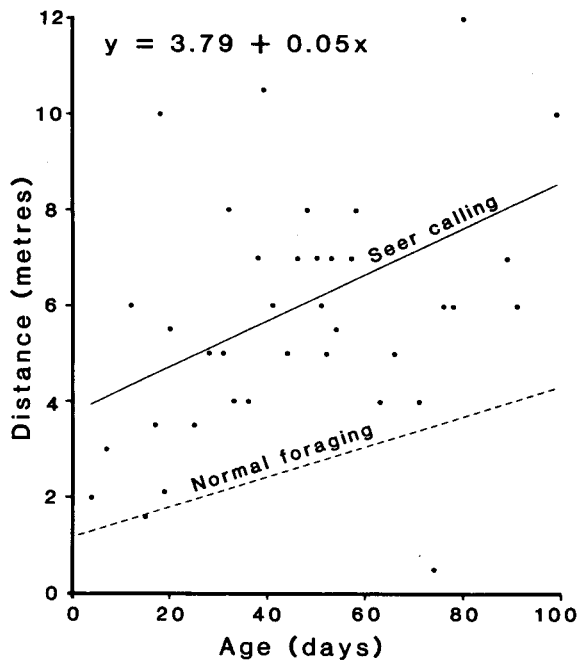

FIG. 5. Median distances between spruce grouse brood hens and their chicks of various ages that were uttering the seer call ($r^2 = 0.13$; $P = 0.031$). Regression line for normal foraging taken from Fig. 4 for comparison.

louder heep call from the brood hen and (or) a movement towards the calling chick. The average distance at which this occurred was significantly greater than that recorded during normal foraging situations ($P < 0.001$; ANCOVA and, likewise, increased with age (Fig. 5). The effect upon brood hens of the seer call was sufficiently strong for them to respond to this call from unrelated chicks as well as to imitations of it by researchers. This response only waned after the chicks were largely grown and on the point of brood breakup.

Keppie (1977) and Alway (1977) suggested that juveniles could recognize their own brood hen. Evidence from this study supports that contention. Despite the occasional mixing of broods, young chicks in this study were never recorded abandoning their live brood hen for another. Only after chicks had lost their brood hen (through death or disappearance at time of brood breakup) did they follow another brood hen that

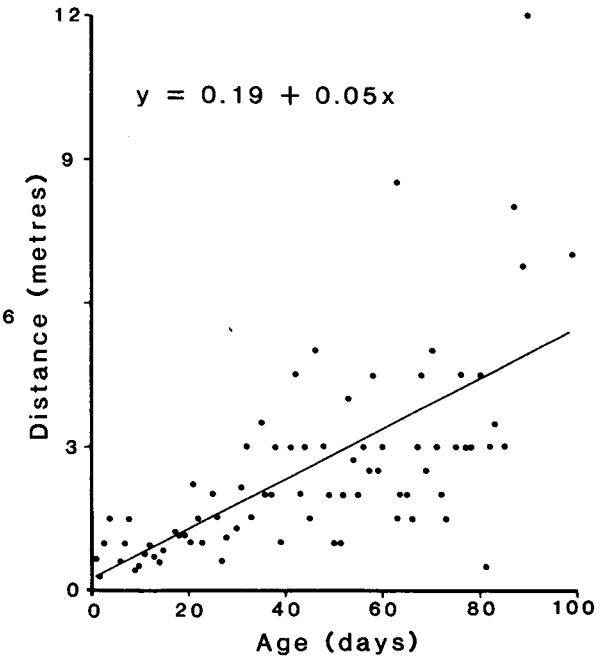

FIG. 6. Median distances between sibling spruce grouse chicks of various ages ($r^2 = 0.40$; $P < 0.001$).

responded to their calls.

As distances between brood hen and chicks increased, so did average distances between nearest siblings (Fig. 6). The increased distances between older siblings are unlikely a response to increasing intersibling or hen–chick aggression, neither of which was observed in the field. If this type of aggression occurs, it must be relatively subtle. Our observations support the suggestions of Alway and Boag (1979) that interindividual distances increase throughout the brood period without any corresponding increase in aggressive interactions. Gradually weakening bonds that hold the brood together, and (or) an increasing physical ability of the juveniles to move around, more adequately explain the increased interindividual distances.

Movements, initiated by the brood hen and followed by the brood, were quite variable in both direction and distance. Brood hens rarely stayed in the same place for more than a few minutes when they were not brooding. When brooding bouts were eliminated from the analysis, a positive relationship between the age of the juveniles and the distance moved while foraging was apparent (Fig. 7). Typical movements were concentrated at the edges of meadows and in areas with a sparse canopy, similar to the observations of McCourt (1969) who found that the canopy cover at locations where broods were sighted was less than at random sites in the forest. Nevertheless, broods often traversed areas of dense cover with little understory, but they did so more rapidly than in other situations (Schroeder 1985*a*).

The purring call was frequently uttered by feeding chicks. It was usually given in open habitats by a chick that was actively feeding on an item that appeared to be a preferred food. In one case a juvenile feeding on a mushroom (Basidiomycetes) gave purring calls that attracted its siblings and mother, whereupon they all fed simultaneously at the same mushroom. Although this call attracted other chicks, it may also have slowed the hen's rate of movement. In all 11 cases in which the distance moved by the hen was noted following chick purring calls, it

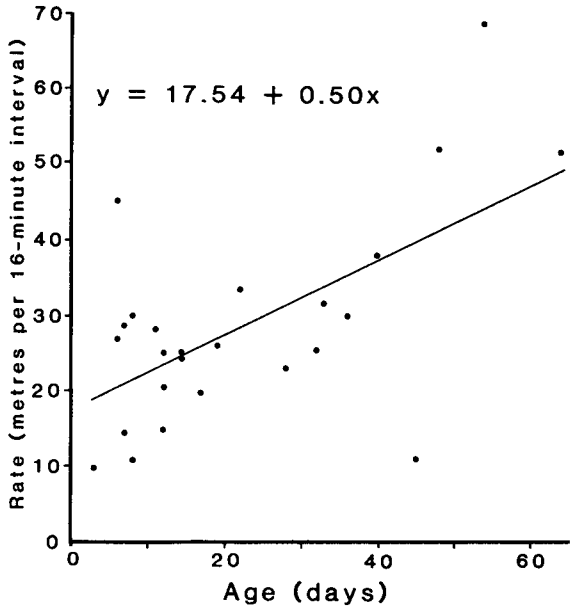

FIG. 7. Rate of movement by spruce grouse broods of different ages through pine forest habitat in southwestern Alberta (periods when brooding occurred were excluded) ($r^2 = 0.38$; $P = 0.001$).

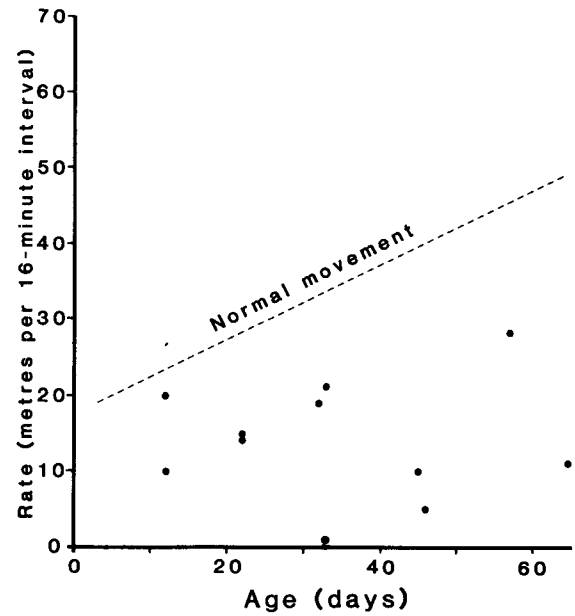

FIG. 8. Rate of movement by spruce grouse broods of different ages through pine forest habitat in southwestern Alberta, immediately after a chick had uttered the purring call. Regression line for normal movement by age taken from Fig. 7 for comparison.

was less than that expected ($P < 0.05$; χ^2 contingency table), based on normal rates of brood movement (Fig. 8). Although the brood hen's slower movement in open areas may be a response to the purring calls of chicks, other factors, such as her perception of good feeding habitat and (or) greater vigilance because of potentially increased vulnerability to predators, could also slow these movements.

As observed by McCourt (1969) and Alway (1977), brood hens typically viewed the foraging brood from elevated positions such as logs. The hens would often remain alert in such locations and respond to chicks with heep calls. If potential predators such as raptors (Accipitrinae), red squirrels (*Tamiasciurus hudsonicus*), or sudden movements of observers were noted, the hen would utter hum calls similar to those recorded as warning calls by Alway (1977). Although Alway recorded an alarm call given in response to more immediate dangers (raptors or closely approaching ground predators) than when the hum call was uttered, such a distinction was not evident in this study. In the case of red squirrels, brood hens were observed on two occasions visually and vocally threatening the squirrel by erecting their feathers, fanning their tail, and charging within 0.5 m of it while uttering what sounded like the cantus (Nugent and Boag 1982). In response to the approach of a researcher, the hen typically uttered the cantus and gave distraction displays if the chicks were less than 2 weeks of age and unable to fly well; first weak flight by a juvenile spruce grouse was observed at 8 days of age (first flight observed at 7 days by Stoneberg (1967), and 14 days by Alway (1977)). The chicks generally responded to hum calls by becoming motionless (or alert) and silent. The response to immediate potential danger frequently included escape behaviour by the chicks (running, flying, and (or) hiding).

Hum calls appeared to be given only by females, both juveniles and adults, as suggested by Alway (1977). The sex-specific use of these calls may be expected if the calls are an important part of the vocal repertoire of brood hens. Among juvenile females the hum call was first recorded at 45 days of age. Females of all ages were heard giving hum calls during the fall, winter, and early spring while in blocks with other related and (or) unrelated spruce grouse. The hum call seemed to have the same effect in flocking situations as it had in broods; it typically elicited silence and immobility among flock members.

Loafing behaviour

Loafing behaviour was a major component of the behavioural repertoire of juvenile spruce grouse (Fig. 2) and specifically included loafing, preening, dust-bathing, and flapping-run behaviours (Table 1). The majority of juvenile loafing time consisted of chicks sitting on the ground in the sunshine. Most preening was also done in such situations. Occasionally juveniles, along with the brood hen, dust-bathed. The earliest a chick was observed dust-bathing was at 6 days of age, similar to that recorded for ruffed grouse (*Bonasa umbellus*) (Maxson 1978) and red grouse (*Lagopus lagopus*) (Watson and Jenkins 1964).

Although previously linked to male juveniles about the time of brood breakup (Alway 1977), the flapping-run behaviour was observed here in chicks as early as 2 days of age. Likewise, intense forms of flapping-run behaviour were observed for both sexes of juveniles and even in a 4-year-old female. In the latter case, the female vigorously displayed the flapping-run behaviour for 30 s after alighting from a tree in which the night had been spent. This behaviour appeared to be contagious among juveniles and was most often observed immediately after loafing or brooding.

Additional behaviour

In addition to brooding, feeding, and loafing, juveniles displayed other behaviour patterns related to intraspecific interactions. Although interactions occurred in the broods observed, they were neither sufficiently overt nor frequent enough to use with confidence in determining dominance hierarchies. The most notable behaviour associated with intraspecific interactions was the jerky-crouch, a behaviour in which the bird crouches close to the ground and jerks its head from side to side

in a lateral arc (Alway 1977). Although Alway observed it frequently in chicks at more than 61 days of age, I observed it four times in chicks 43–48 days old. On two occasions a juvenile female gave the jerky-crouch when approached closely by her brood hen. The other two occurred among juvenile males, apparently in response to a closely approaching male sibling that was displaying. All four situations appeared to be similar to those observed by Alway (1977) and may have been a subordinate bird's response to a more dominant individual.

Like the jerky-crouch, the display-walk with tail-swaying and rush with momentary tail-fanning (Hjorth 1970) were both observed first in a 45-day-old male, considerably earlier than when first observed in captivity in 90-day-old juvenile males (Alway 1977). Although the example from this study apparently occurred as part of an interaction (within a brood of four males), the same behaviours were observed by males with at least one female nearby. Agonistic interactions among juveniles were not common at any time of the brood period, including brood breakup (median of 4 September for males and 15 September for females; Schroeder 1985*a*). They were seldom observed and were apparently spread throughout the entire brood period.

Discussion

Brooding bouts, which were characteristic of early brood behaviour, appeared to be initiated by chick sury calls and ended by sreep calls. Although unrecorded by Alway (1977), sury calls were similar to sreep calls except for their slightly longer duration and ascending pitch. It is possible that the hen stopped brooding the chicks when their sury calls ceased, perhaps an indication that the chicks were no longer cold. In any case, individual chicks occasionally moved out from beneath the brood hen before she stood up, a situation very similar to that observed in wild blue grouse (Zwickel 1967).

As the thermoregulatory capacity of chicks increased with age, their dependency on brooding decreased. The maximum age at which chicks were brooded in this study was compared with those recorded in other galliformes: 10 to 12 days for domestic fowl (*Gallus gallus*) (Wood-Gush 1955), 6 days for rock ptarmigan (*Lagopus mutus*) (Theberge and West 1973), 56 days for white-tailed ptarmigan (*Lagopus leucurus*) (K. M. Giesen, personal communication), 6 (Allen *et al.* 1977), 14 (Aulie 1976), and 42 days (Watson and Jenkins 1964) for willow ptarmigan (*Lagopus lagopus*), 11 days for blue grouse (Zwickel 1967), and 20 days for spruce grouse (Alway 1977). Even if the example of brooding at 50 days in this study of spruce grouse is disregarded, brooding from 20 to 40 days was still relatively common (Fig. 2). Of the above examples, only brooding at 42 days by willow ptarmigan and 56 days by white-tailed ptarmigan were observed in the field. Captive spruce grouse stopped brooding at 20 days of age (Alway 1977), perhaps in response to milder conditions (>10°C) in the aviary than those apparently associated with brooding by old chicks (>20 days old) in the wild (Fig. 1). The influence of environmental conditions on brooding frequency has also been shown for willow ptarmigan (Aulie 1976; Boggs *et al.* 1977; Pedersen and Steen 1979; Erikstad and Spidso 1982).

Although the frequency of brooding behaviour decreased with increasing chick age, age did not appear to affect the median duration of 11 min for brooding bouts. Pynnonen (1954) also found that wild hazel grouse (*Bonasa bonasia*) brooded for periods of 10 to 20 min. Pedersen and Steen (1979), however, observed brooding bouts in willow ptarmigan that varied between 3 and 30 min but decreased with age.

The cohesion of broods in this study appeared to be maintained by the heep calls of brood hens and the sreep and seer calls of chicks. Hen–chick and intersibling distances increased throughout the brood season. Likewise, the hen–chick distances required to elicit a seer call by the chicks also increased with age. This was similar to the situation observed with captive spruce grouse (Alway 1977) and with wild blue grouse (Zwickel 1967). As broods approached the time of brood breakup, hens appeared less likely to respond to the sreep and seer calls of juveniles. After the brood hen was separated from the brood (brood breakup), the chicks often remained together, apparently remaining in contact with each other using the sreep calls. This, and the fact that unrelated brood hens may still respond to sreep and seer calls, may help explain why larger "gang" broods form in the fall (Keppie 1977).

A notable lack of aggressive interactions at the time of brood breakup suggests that interactions are probably not important in actually causing the breakup. Bowman and Robel (1977) attributed increased intersibling distances in broods of greater prairie chickens (*Tympanuchus cupido*) to increased aggressiveness among them at the time of brood breakup. Although Alway and Boag (1979) observed an increase in aggressive interactions in October among captive juveniles, broods generally would have broken up by this time in the wild. Additionally, a high frequency of aggressive interactions, such as those observed by Watson and Jenkins (1964) in red grouse and Alway and Boag (1979) in spruce grouse, may be an artifact of captivity. Field situations permit the essentially unrestricted movement of chicks and consequently they may easily avoid direct interactions (Zwickel 1967). Although the observations for spruce grouse in the field do not eliminate the potential importance of aggressive interactions within broods, they do indicate that other factors, such as the decreasing cohesion of the brood, may be more important in explaining the timing of brood breakup.

Acknowledgments

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