The fall phase of dispersal in juvenile spruce grouse

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Received January 31, 1985

SCHROEDER, M. A. 1986. The fall phase of dispersal in juvenile spruce grouse. Can. J. Zool. **64**: 16–20.

The characteristics of the fall phase of dispersal for 41 female and 88 male juvenile spruce grouse (*Dendragapus canadensis*) were analyzed for data collected between 1965 and 1984 in southwestern Alberta. Females moved significantly farther than males. Reasons for this difference were sought in location of wintering areas, timing of brood breakup relative to that of brood hen migration, and distance moved by the migrating brood hen. Wintering areas, encompassing blocks of forest within which more than 80% of adults passed the winter, represented less than 15% of the study area. These areas were apparently also the destination for a high proportion (84%) of the juveniles. Distances moved are believed to be influenced by the location of the wintering areas in relation to the direction taken by juveniles after brood breakup occurs, as well as the timing of this event in relation to the timing of migration in adult hens. Brood breakup of juvenile males preceded that of females (median 4 and 15 September, respectively), and dates of brood hen migration overlapped those of brood breakup (median 13 September). Hence, longer distances moved during the fall phase of dispersal (and a greater disappearance rate) by juvenile females relative to males may be caused by their later median date of brood breakup and consequently the increased probability of their moving with their migrating brood hens. This possibility is supported by the observation of intact broods following the migratory paths of their mothers. The data suggest that once the brood breaks up, juveniles may stop at nearby wintering areas.

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L'accumulation de données recueillies entre 1965 et 1984 dans le sud-ouest de l'Alberta a permis de procéder à l'analyse des caractéristiques de la dispersion d'automne chez 41 femelles et 88 mâles immatures de tétras du Canada (*Dendragapus canadensis*). Les femelles couvrent des distances significativement plus grandes que les mâles. Les raisons possibles de cette différence ont été examinées: situation des aires d'hiverage, moment de la rupture de la couvée relativement au moment de la migration de la mère et distance parcourue par la mère au cours de sa migration. Les aires d'hiverage, qui recouvrent des blocs de forêts dans lesquels plus de 80% des adultes passent l'hiver, représentent moins de 15% de l'aire d'étude. Ces aires sont aussi apparemment la destination d'une grande proportion (84%) de jeunes. Les distances parcourues semblent être influencées par la situation des aires d'hiverage en rapport avec la direction qu'empruntent les jeunes à la rupture de la couvée, de même que par la moment de cette rupture en relation avec la moment de la migration des femelles adultes. La rupture des couvées se fait plus tôt pour les jeunes mâles (médiane le 4 septembre) que pour les jeunes femelles (médiane le 15 septembre) et la date de migration des mères chevauche le moment de la rupture des couvées (médiane le 13 septembre). Les distances significativement plus grandes que parcourent les jeunes femelles au cours de leur dispersion d'automne (et leur taux de disparition plus élevé) peuvent être attribuables à leur départ plus tardif et, conséquemment, à la probabilité plus grande qu'elles se déplacent avec les mères migratrices. Cette hypothèse est corroborée par l'observation de couvées entières qui suivaient les routes de migration de leurs mères. Les données semblent indiquer qu'après la rupture des couvées, les jeunes peuvent s'arrêter dans les aires d'hiverage avoisinantes.

[Traduit par le journal]

Introduction

The dispersal of spruce grouse, *Dendragapus canadensis*, from their place of hatch to their place of breeding or attempted breeding is divided into two discrete phases: fall and spring (Keepie 1975). The two phases are separated by a winter period during which relatively little movement occurs. Keppie (1975) found that the fall emigration rate of juvenile males (41%) was significantly lower than that of females (75%), and suggested that the higher emigration rate of females was probably related to their greater overall fall dispersal distances. Apart from documentation of fall movements in juvenile spruce grouse, the cause of the observed variability between sexes, such as with distances moved, has been suggested to be the result of intraspecific interactions and (or) innate behavioural differences (Herzog and Boag 1977, 1978; Alway and Boag 1979; Keppie 1979, 1980). Although Keppie (1975) observed juveniles moving with their migrating brood hens, the date of brood breakup in relation to the timing of adult female migration was not examined. Since a large proportion of brood hens is migratory (55% according to Herzog and Keppie 1980), and dates of migration and brood breakup may overlap, timing of dispersal may influence distances moved, and deserves consideration. Another factor that may influence the fall phase of dispersal in juvenile spruce grouse is the probability of encountering patches of winter habitat that would bring dispersing birds to a stop. The extent to which juveniles move with their migrating mother may also be an important aspect in whether they stop in the first wintering areas encountered.

This paper reexamines dispersal distances and disappearance rates of juvenile spruce grouse during the fall. Previously ignored aspects of juvenile and brood hen behaviour at the time of brood breakup, as well as possible concentrations of wintering grouse, are considered because of their potential influence on fall movements.

Methods

Spruce grouse have been censused and (or) radio tracked from 1965 to 1985 near the R. B. Miller Biological Station (50°39′ N, 114°39′ W), 27 km west of Turner Valley, Alberta. The main study area consisted of 555 ha of forest dominated by lodgepole pine (*Pinus contorta*), with scattered clumps of white spruce (*Picea glauca*) and poplar (*Populus* spp.).

Birds were noosed (Zwickel and Bendell 1967) and marked with colour-coded leg bands. Radio transmitters were attached to females in 1974–1975, 1977, and 1980–1984, and to juveniles in 1975 and 1982–1983. Locations of birds were plotted using a large grid system superimposed over air photos.

Grouse were categorized as juveniles (<6 months), yearlings (6–15 months), or adults (>15 months). Designation of seasons was based on

aspects of behaviour, such as movements and dispersion (Herzog and Boag 1978), and timing of migration and dispersal (Herzog and Keppie 1980), and were as follows: winter, 16 October – 31 March; and summer, 16 May – 15 August. These designations with up to 2 months between them enabled me to avoid confusion between early and late movements, either dispersal or migration, and normal daily movements within summer or winter ranges.

Median dates for the initiation of adult migration in the fall were determined by examining daily locations of radio-tagged adult females only (not all radio-tagged females were tracked daily). The intensity of search effort on the study area exceeded that beyond its artificial boundaries, and consequently it was necessary to distinguish birds that remained on the area from those that moved off the area for part of the year. Any adult female having both winter and summer ranges on the study area was classed as an on-area migrant, whereas those crossing the boundaries of the study area were classed as off-area migrants. Brood breakup dates for juveniles were designated as the midpoint between a bird's last sighting in the brood and its first sighting away from the brood hen (only those cases for which the interval was 14 days or less were considered).

Dispersal distances of juveniles in the fall were determined for each bird by calculating the straight-line distance between the median locations (median of x and y coordinates) of all sightings on their brood and winter ranges. The median values were used to reduce the statistical influence of outlier points. Disappearance rates were calculated by dividing the number of juveniles missing from the study area in winter by the number of juveniles known to be alive on the study area in late summer. A mortality rate of 15% for the 2-month period during and after brood breakup, based on the death of 4 of 27 radio-marked birds, was incorporated into the estimate. The data used for calculating fall disappearance rates were only compiled for those years in which the main area was thoroughly censused using evenly spaced transects during both summer and winter (1970–1973, 1982–1983). Other data on dispersal distances were analyzed for all years. Most birds residing on the study area were probably found by censusing (Boag and McKinnon 1982), because almost all radio-tagged birds on the study area were found using normal censusing techniques in addition to radiotelemetry.

For adults, locations of areas used by grouse in winter were determined by plotting on a map the median wintering locations (based on a minimum of three sightings). Wintering areas were delineated when the median locations of three or more adult grouse occurred in a cluster in which the distance between neighbours did not exceed 80 m (mean radius of the winter range of radio-tracked adults; Herzog and Boag 1978). A perimeter was drawn around each cluster enclosing all its median locations as well as a boundary area extending 80 m from the outer medians of the cluster, thus encompassing the area used by peripherally located birds.

Results

Characteristics of the fall phase of dispersal

Dispersal distances for juvenile spruce grouse during the fall ranged up to at least 6 km (Fig. 1). Based on data from juveniles without radios, there was no difference in distances moved by males and females, but females moved further than males when only radio-tracked juveniles were considered (Table 1). The lack of a statistical difference among juveniles without radios suggests that the study area was too small relative to many dispersal movements. Birds moving off the study area would be difficult to find without the use of radiotelemetry. The disappearance rate of females (75.8%; n = 103) was significantly higher ($P < 0.001$; χ^2 contingency table) than that of males (52.1%; n = 114). Both rates were similar to those recorded by Keppie (1979). The high disappearance rate of females supports the previous result that radio-tracked females move further than males and thus out of range of normal censusing on the study area.

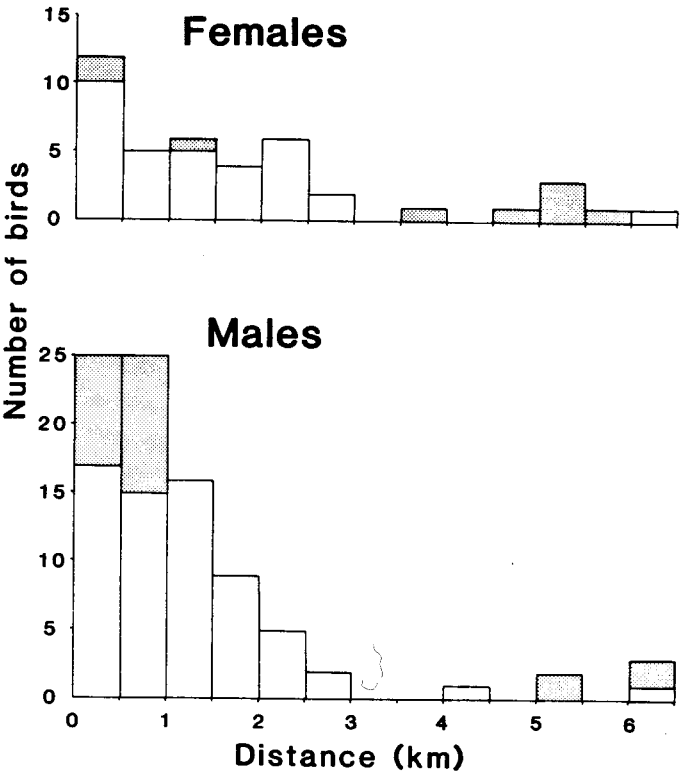

FIG. 1. Distribution of distances for the fall phase of dispersal for female (n = 42) and male (n = 88) juvenile spruce grouse in southwestern Alberta, 1965–1984. ▦, radio-tracked juveniles; □, juveniles without radios.

TABLE 1. Median distances (metres) for the fall phase of dispersal for juvenile spruce grouse in southwestern Alberta

Category	Male (n)	Female (n)	P*
Radio-tracked juveniles	650 (22)	4974 (9)	0.048
Juveniles without radios	1059 (66)	1085 (33)	0.447

*Mann–Whitney U-test (2-tailed).

Association with wintering areas

Wintering areas covered less than 15% of the study area (Fig. 2) yet enclosed 81% of all median locations of winter adults (n = 225). The remaining 19% of the median locations were of single birds (and hence did not qualify for the definition of a wintering area) scattered widely throughout the rest of the study area. Similarly, 81% of juvenile males (n = 91) and 86% of juvenile females (n = 87) had median winter locations within the boundaries of wintering areas. The 15 wintering areas delineated on the study area each contained the median winter locations of an average of 15 adults and 12 juveniles. Juvenile males did not differ from females in their proximity to wintering areas ($P > 0.10$; χ^2 contingency table). However, both had their median locations on wintering areas more frequently than would be expected if they were distributed randomly throughout the study area ($P < 0.001$ for both males and females; χ^2 contingency table).

Timing of the fall phase of dispersal

The median date of migration for brood hens was 13 September (range 3 August – 18 November; n = 14). The median brood breakup date for juvenile females (15 September;

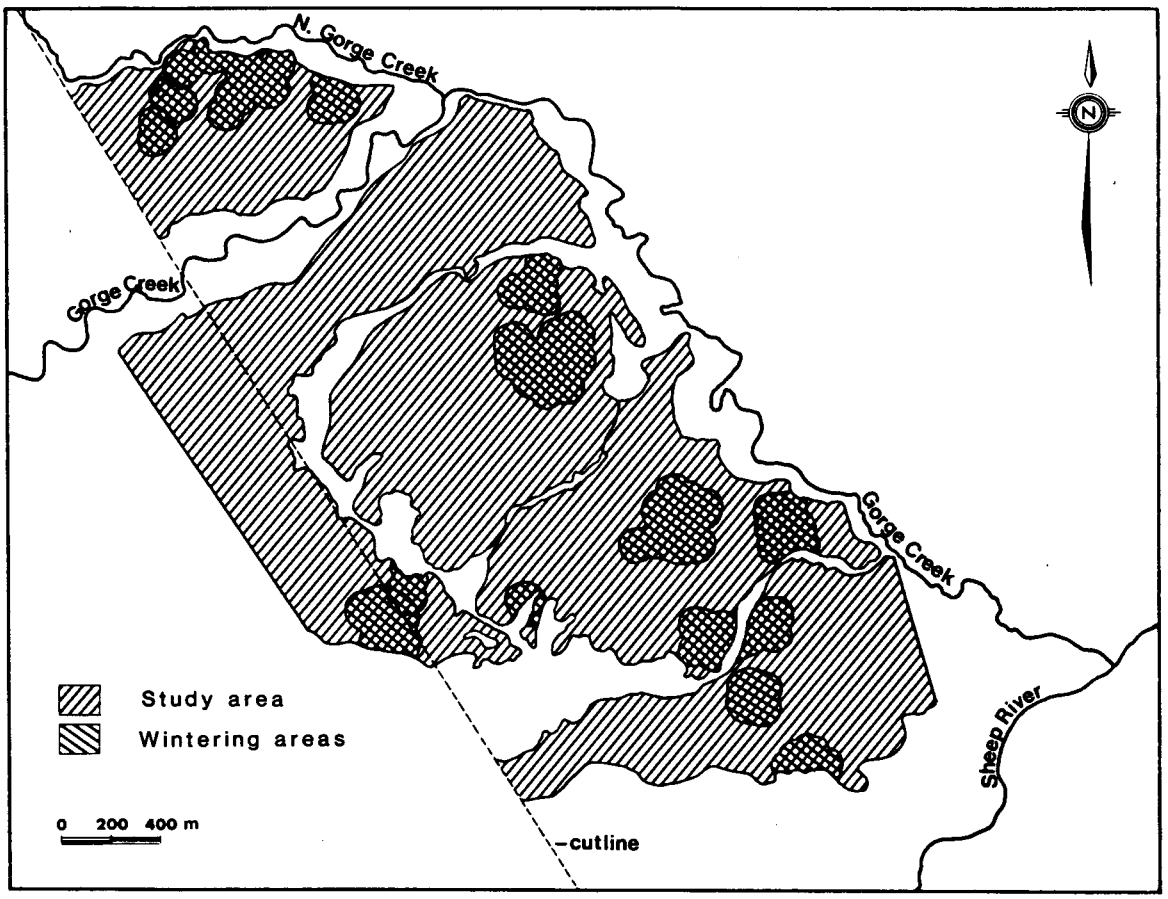

FIG. 2. Location of spruce grouse wintering areas on the southwestern Alberta study area. Cutline, ca. 15 m wide grassy right-of-way.

range 8 August – 26 October; n = 33) was significantly later (P = 0.026; Mann–Whitney U-test) than that for juvenile males (4 September; range 13 August – 23 October; n = 46). The difference between the sexes in date of brood breakup, and the fact that date of brood hen migration overlaps that of brood breakup, suggest the potential importance of the relative timing of the two events in the observed patterns of the fall phase of dispersal (Fig. 3). If some brood hens were to migrate before their chicks left the brood, the resulting fall dispersal distances of their juveniles would probably be larger than they would be if the hen migrated after brood breakup.

In this study 47% of the adult females on the study area in the summer migrated off the area in the fall (15 of 32 radio-tracked females). The median off-area migration distance of 2.9 km (11 km was the maximum recorded; Schroeder 1985*a*) was greater than the median on-area distance of 0.4 km (P = 0.007; Mann–Whitney U-test). Since juvenile females have a later date of brood breakup than males, they would be more likely to move off the study area with their mothers, a movement which would tend to be additive to both their fall dispersal distances and emigration rate. Conversely, the relatively small fall dispersal distances of juvenile males (median of 650 m) may suggest that the earlier date of male brood breakup precludes their moving with their migrating mothers. Despite the previous observations of juveniles with migrating brood hens (Keppie 1975), the importance of these movements on the disappearance rates and fall dispersal distances of juveniles has not been considered.

A more detailed analysis of emigrants or off-area dispersers supports the above suggestions. Of 28 juveniles that dispersed more than 2 km (a typical dispersal distance that would take them off the study area), 20 had known off-area migrant brood hens; the status of the brood hens of the remaining 8 was unknown. For the 13 juveniles moving more than 3 km, all had off-area migrant brood hens (13 chicks among seven different broods). Of these 13, 10 (6 females and 4 males) had radio-tracked brood hens (4 different hens) and all 10 were known to have moved with their migrating mothers. No juveniles that had brood breakup before their brood hen's migration were known to disperse more than 2 km in the fall.

Discussion

The existence of areas where adult spruce grouse concentrate in winter, although previously unrecorded and generally relatively small in size, may be very important in influencing the settlement of juveniles in winter. Restricted areas of preferred winter habitat, as suggested by Ellison (1976), Herzog (1977), Paterni (1979), Herman (1980), and Robinson (1980), and the formation of winter flocks, as described by Ellison (1973) and Keppie (1975), may be primary factors influencing the use of space in winter. The evidence presented here shows that juveniles were not randomly distributed in winter but were associated with the same areas used by wintering adults. This association may reflect a tendency of juveniles to flock with other spruce grouse and (or) to select the same habitat.

The association of juveniles with specific wintering areas suggests that dispersal distances and disappearance rates in the fall could reflect the availability of these areas along the paths of

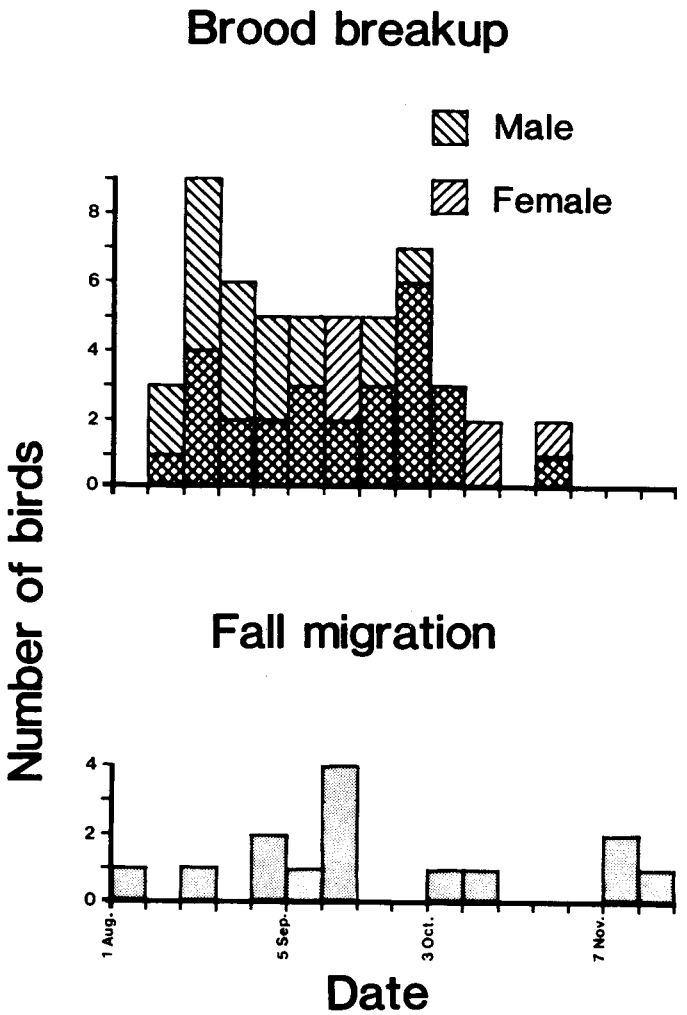

FIG. 3. Distribution of dates of brood breakup for juveniles and dates of fall migration for radio-tagged brood hens in southwestern Alberta.

dispersing birds. However, even if wintering areas are used as destinations for moving juveniles, they do not fully explain the large disappearance rates. Moreover, they do not provide a possible explanation for sexual differences in disappearance rate and dispersal distance.

Examination of the timing of events during the brood breakup and fall dispersal period provides a possible explanation for characteristics of the fall phase of dispersal in spruce grouse. The overlap in the timing of brood breakup and brood hen migration suggests that it may be relatively common for juveniles to move with their migrating brood hens (a large percentage of females probably migrate before their broods break up). Field observations of juveniles accompanying their migrating mothers (Keppie 1975; this study) agree with this suggestion, and explain why variation in dispersal distances within broods may be less than among them (as shown for males by Keppie 1980). Analysis of distances of dispersal during the fall for radio-tracked juveniles shows that females move significantly farther than males. Similarly, females have significantly greater disappearance rates than males. The proportionally longer movements made by females than males support Keppie's (1979) speculations on sex-biased dispersal based on emigration rates alone. The fact that females leave the brood later than males, and that juveniles may accompany their migrating brood hen if migration precedes brood breakup, may be a reason for the difference in distance moved and disappearance rate for the two sexes. The significance of this phenomenon is that migrating brood hens would be more likely to migrate in the company of their female than their male chicks.

The most apparent and potentially important factors affecting the fall phase of dispersal in juvenile spruce grouse were examined in this study. Additional factors not considered in this study may also be operating. For example, dominance–subordinance interactions within a sex or age class may influence the spatial organization of spruce grouse in the winter. Intraspecific interactions have been observed in the field (Schroeder 1985*b*), but their implications for spacing behaviour are so far based on indirect evidence (Ellison 1973; Herzog and Boag 1978; Alway and Boag 1979).

Alway (1977) suggested that dominance hierarchies, possibly formed in the brood, may have an effect on patterns of dispersal, such as distances moved. However, he observed few aggressive interactions until after the fall dispersal period, and suggested that nonaggressive behavioural differences among juveniles were probably more important in causing differences in fall movements. Similarly, Keppie (1979) found that the fall phase of dispersal was not related to grouse densities, apparently because of equal emigration and immigration. If movement were influenced by aggressive interactions, a positive relationship between density and distance or emigration rate would be expected because of the increased probability or necessity of encountering conspecifics. Additionally, Keppie's (1980) observation of lesser variability within broods than among them for male fall dispersal distances may support the idea that a genetic component of behaviour might explain the observed variability. However, the variability observed by Keppie may also be explained by the sharing of similar environments by members of each brood, such as the quantity or quality of wintering areas near the brood's summer range. Likewise, variation in attributes of the brood hen such as hatch date (age of the juveniles) and behaviour associated with brood cohesion or migration, would produce the same effect.

The fall phase of dispersal is characterized by a movement in which females move both farther and more frequently than males. It is not known whether the increased movement of females plays an important part in increasing gene flow (Howard 1960; Johnston 1961; Murray 1967), colonizing suitable habitats (Dice 1952), or regulating the population size (Errington 1956; Lidicker 1962; French *et al.* 1968; Christian 1970; Myers and Krebs 1971). Despite the lack of information on the ultimate consequences of the fall phase of dispersal, the observations from this study suggest that the location and timing of brood breakup and location of wintering areas are proximal factors that could influence the nature of the dispersal movement. If juvenile spruce grouse can be shown to stop at the first-encountered wintering area after brood breakup, it would suggest that other factors such as dominance–subordinance interactions or innate differences in dispersal tendencies are of lesser importance than destination areas in affecting the patterns of fall dispersal.

Acknowledgements

I am grateful to P. Angelstam, D. A. Boag, W. G. Evans, S. J. Hannon, J. E. Hines, I. G. Jamieson, D. M. Keppie, D. T. McKinnon, S. G. Reebs, R. F. Ruth, J. B. Theberge, J. M. Waterman, and F. C. Zwickel for reviewing previous versions of this manuscript. I also thank J. M. Waterman for preparing

the figures and V. C. Brown, S. G. Reebs, and I. M. Wishart for assistance with the fieldwork. Much of this research could not have been done without the help of my supervisor, D. A. Boag, and access to the data collected by his previous students, R. A. McLachlin, K. H. McCourt, D. M. Keppie, P. W. Herzog, D. P. Nugent, K. E. Smyth, and D. T. McKinnon. Financial assistance was provided by the Boreal Institute for Northern Studies, The University of Alberta, and a Natural Sciences and Engineering Research Council of Canada grant (A2010) to D. A. Boag.

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