LITERATURE CITED

BARNETT, B. D. AND R. L. RUDD. 1983. Feral dogs of the Galapagos Islands: impact and control. Int. J. Stud. Anim. Prob. 4:44–58.

BOERSMA, P. D. 1974. The Galapagos Penguin: a study of adaptations for life in an unpredictable environment. Ph.D. diss., Ohio State Univ., Columbus, Ohio.

———. 1977. An ecological and behavioral study of the Galapagos Penguin. Living Bird 15:43–93.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. No. 72.

HARRIS, M. 1974. A complete census of the Flightless Cormorant. Biol. Conser. 6:189–191.

———. 1979. Population dynamics of the Flightless Cormorant. Ibis 121:135–145.

RALPH, C. J. AND J. M. SCOTT (eds.). 1981. Estimating numbers of terrestrial birds. Stud. Avian Biol. 6.

ROSENBERG, D. K. AND S. A. HARCOURT. 1987. Potential conservation problems of the endemic Galapagos Penguin and Flightless Cormorant. Noticias de Galapagos 45:24–25.

SEBER, G. A. F. 1986. A review of estimating animal abundance. Biometrics 42:267–292.

VALLE, C. A. AND M. C. COULTER. 1987. Present status of the Flightless Cormorant, Galapagos Penguin, and Flamingo populations in Galapagos after an El Niño year. Condor 89:276–281.

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Female-female aggression in White-tailed Ptarmigan and Willow Ptarmigan during the pre-incubation period.—Aggression among female birds usually is less conspicuous than among males. Focus on female behavior, however, has revealed that female-female aggression is directed toward defense of space (Herzog and Boag 1977), nest sites (Gowaty 1981, Leffelaar and Robertson 1985), and/or mates (Jenkins 1961, Yasukawa and Searcy 1982, Petrie 1986, Hobson and Sealy 1989) and may be critical in shaping the social system. More specifically, active monopolization of mates by females was hypothesized by Wittenberger and Tilson (1980) to be a factor that could maintain a monogamous mating system. Monogamy is the predominant mating system for both White-tailed Ptarmigan (*Lagopus leucurus*) and Willow Ptarmigan (*L. lagopus*) (Wittenberger 1978). In both species, males accompany females almost constantly until onset of incubation. White-tailed Ptarmigan males remain with the hen through early and mid-incubation, accompanying her when she is off the nest. Once the eggs hatch, the male plays no part in brood rearing, contrary to the Willow Ptarmigan where males remain with broods until autumn (Wittenberger 1978). Aggressive interactions between female ptarmigan have been observed during the breeding season, principally before the onset of incubation. MacDonald (1970) and Hannon (1983) showed that paired female Rock Ptarmigan (*L. mutus*) and Willow Ptarmigan, respectively, threatened and/or attacked "intruding" models of females during spring. Whether this aggression was for the purpose of defending a territory or monopolizing a mate was not determined. Regardless, males would have a more difficult time acquiring second mates. Hannon (1984) suggested that territorial hen ptarmigan prevent potential secondary hens from settling on the same site in spring, and thus a monogamous pairbond is maintained by female-female aggression. If this hypothesis is to provide a general explanation for the maintenance of monogamy in ptarmigan, one would predict similar levels of female-female aggression in other populations of Willow Ptarmigan and in the two other closely related ptarmigan species. The purpose of this study was to examine levels of female-female aggression during the pre-incubation period in other ptarmigan populations. We presented female models to female White-tailed Ptarmigan in Colorado and to Willow Ptarmigan in Manitoba. We also re-examined Hannon's data for Willow Ptarmigan in British Columbia, and report relevant data from a Rock Ptarmigan study in Nouveau Québec.

Study areas and methods.—Models were presented to female ptarmigan from mid May to early June, after pairing and before laying. Presentations, by Lord and Martin, to female White-tailed Ptarmigan were at Mt. Evans and Loveland Pass, Colorado (CO) in 1987 and 1989. Presentations in 1986 by Martin were to female Willow Ptermigan at LePérouse Bay (LPB), Manitoba. Hannon's 1980–82 presentations were at Chilkat Pass (CP), British Columbia and were described earlier (Hannon 1983).

We set a model of a hen ptarmigan in breeding plumage and in semi-alert posture within 20 m of a hen and guided the female toward it until we were sure she could see the model. We then moved away, waited 5 min, and recorded her behavior for 10 min (5 min by Hannon). As a control, Hannon presented a stuffed female Bufflehead (*Bucephala albeola*) at CP, and Lord and Martin used a milk carton; both controls were similar in size to ptarmigan but did not resemble either a conspecific or a potential predator. No control was used by Martin at LPB. Models were presented once to each hen. We recorded whether females ignored or approached the model or control, the closeness of the approach, and the number of attacks and vocalizations (territorial and aggressive calls). To test for independence of behavioral responses between populations, sampled randomization tests (N = 500) were used (Sokal and Rohlf 1981), and G_{ran} values reported.

Results and discussion.—Responses of females to the female models varied from no response to direct attack and were ranked in order of increasing intensity from 1 to 4 (Table 1). The three populations of female ptarmigan differed in their responses to the models ($G_{ran} = 36.97$, df = 6, $P < 0.0001$). This heterogeneity was due to differences in responses both between and within species. White-tailed Ptarmigan females (CO) were less aggressive to the models than Willow Ptarmigan hens (CP and LPB combined) ($G_{ran} = 28.39$, df = 3, $P < 0.001$). Female Willow Ptarmigan were less aggressive in Manitoba (LPB) than in British Columbia (CP) ($G_{ran} = 8.57$, df = 3, $P = 0.05$). The proportion of hens that vocalized (territorial or threat calls) to the models varied among the three populations: 19% of 27 hens at CO, 59% of 17 hens at LPB, and 96% of 23 hens at CP vocalized ($G_{ran} = 35.01$, df = 2, $P < 0.001$). Most hens did not respond to control models, and hens with a rank = 2 did not vocalize or approach closely (Table 1). Female Willow Ptarmigan at CP were more responsive to the ptarmigan model than to the duck model ($G_{ran} = 20.73$, df = 3, $P < 0.0001$). Female White-tailed Ptarmigan also did not respond in any obvious manner to the control model, but since only five of 27 hens approached the ptarmigan model closely, the responses of the CO hens did not differ between the female and control model presentations ($G_{ran} = 6.76$, df = 3, $P = 0.11$).

Response to the ptarmigan model did not vary among age classes of female in any population. At CO, 14 adult hens had a mean response of 1.9 ± 0.3 [SE] while 10 yearling

TABLE 1

RESPONSES OF FEMALE PTARMIGAN TO FEMALE MODEL PRESENTATIONS[a]

Model	Rank of female response[b]				
	1	2	3	4	N
L. leucurus (CO)	12 (44.5)	10 (37)	3 (11)	2 (7.5)	27
Control (CO)	11 (79)	3 (21)	0 (0)	0 (0)	14
L. lagopus (LPB)	2 (12)	4 (24)	9 (53)	2 (12)	17
L. lagopus (CP)	0 (0)	2 (9)	11 (48)	10 (43)	23
Control (CP)	3 (60)	2 (40)	0 (0)	0 (0)	5

[a] N = total number of presentations; numbers in parentheses are the percentages of females giving a certain response.

[b] 1 = no response, bird continues to feed, preen, or sit as she had been doing previous to our approach, no alert posture; 2 = approach to > 1 m but less than 10 m, female in semi-alert or alert posture; 3 = approach to < 1 m, often circles model in alert posture; 4 = attack.

hens had a mean rank of 1.8 ± 0.3 (t = 0.15, df = 22, ns). At LPB, five adult hens had a mean response of 2.2 ± 0.4, while two yearling females had a mean rank of 3.0 ± 0.0 (t = 1.3, df = 5, ns). At CP, 14 adult females had a mean response of 3.4 ± 0.2, and seven yearling hens had a mean rank of 3.3 ± 0.3 (t = 0.26, df = 19, ns).

We observed natural aggressive encounters, involving chases and threats, between neighboring monogamous and co-resident polygamous Willow Ptarmigan hens at both LPB and CP, although less frequently at LPB. Encounters between White-tailed Ptarmigan females are rare during the pre-incubation period (Schmidt 1988, C. E. Braun pers. comm.). During 1987 and 1989, we observed only one natural encounter at CO between two polygamous hens; the dispute, involving a chase and "flight screams" (Schmidt 1988), was short and was terminated when their mate escorted one of the hens away. Thus, with natural observations and by using model presentations, we have observed a similar repertoire of female aggressive behaviors for the three ptarmigan populations. However, the frequency and intensity of these aggressive behaviors varied within populations and between species.

Variation in the extent to which resources such as food, territory, or mates are limiting could explain the differences in levels of female-female aggression we observed among the three populations. For instance, Jenkins (1961) reported increased agonistic interactions among female Gray Partridges (*Perdix perdix*) when numbers of mates were limited. Unmated males occur in most ptarmigan populations (Braun and Rogers 1971, Hannon 1983, Martin 1984, Olpinski 1986, Brodsky and Montgomerie 1987). Hence, levels of female-female aggression likely are not explained by shortages of males in these species. However, there may be shortages of quality males or territories, and this, as yet, has not been tested.

Another potential factor influencing aggression is breeding density. Densities (breeding pairs/km^2) at the time of the model presentations were: CO 1.6, LPB 10, CP 40–50. Thus, observed levels of female aggression were higher with increased breeding density. Levels of aggression tend to increase with increased densities in other species (Moss and Watson 1980, Krebs 1985). In some male birds, testosterone levels, which are related directly to levels of aggression, increase directly with encounter rates (Wingfield 1989). Whether this occurs in females is unknown. Ptarmigan populations fluctuate in density over time. Breeding pairs per square kilometer have varied at CO from 0.8 to 4.6 (Braun and Rogers 1971, C. E. Braun pers. comm.), at LPB from 5 to 10 (Hannon et al. 1988), and at CP from 20 to 50 (Hannon et al. 1988). It would be useful to continue these presentations over several years and look for relationships between density and levels of aggression within populations. In particular we would like to examine levels of female–female aggression in a population of White-tailed Ptarmigan where densities are comparable to those observed for Willow Ptarmigan at LPB.

Finally, our results may reveal differences in levels of female-female aggression between the ptarmigan species that may or may not relate to differences in breeding density. In a population of Rock Ptarmigan in Nouveau Québec with breeding densities of 8.5–9.8 pairs/km^2, Olpinski (1986) observed no aggression by females towards a hen model in a total of 50 trials during and after pairbonding. However, on Bathurst Island, MacDonald (1970) observed a hen Rock Ptarmigan attack a female model; densities were not reported for this study. Neither of the above studies reported instances of natural aggressive encounters between females. Hence, female Willow Ptarmigan may use overt aggression to exclude other females from their territory or their mate, as suggested by Hannon (1983, 1984). White-tailed Ptarmigan and Rock Ptarmigan females may rely on other behaviors, or encounters may be so infrequent that female-female aggression is not a prominent part of their behavioral repertoire during the pre-incubation period.

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LITERATURE CITED

BRAUN, C. E. AND G. E. ROGERS. 1971. The White-tailed Ptarmigan in Colorado. Colorado Div. Game, Fish and Parks. Tech. Publ. 27.

BRODSKY, L. M. AND R. D. MONTGOMERIE. 1987. Asymmetrical contests in defence of rock ptarmigan territories. Behav. Ecol. Sociobiol. 21:267–272.

GOWATY, P. A. 1981. Aggression of breeding Eastern Bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. Anim. Behav. 29:1013–1027.

HANNON, S. J. 1983. Spacing and breeding density of Willow Ptarmigan in response to an experimental alteration of sex ratio. J. Anim. Ecol. 52:807–820.

———. 1984. Factors limiting polygyny in the Willow Ptarmigan. Anim. Behav. 32:153–161.

———, K. MARTIN AND J. O. SCHIECK. 1988. Timing of reproduction in two populations of Willow Ptarmigan in northern Canada. Auk 105:330–338.

HERZOG, P. W. AND D. A. BOAG. 1977. Seasonal changes in aggressive behavior of female Spruce Grouse. Can. J. Zool. 55:1734–1739.

HOBSON, K. A. AND S. G. SEALY. 1989. Female-female aggression in polygynously nesting Yellow Warblers. Wilson Bull. 101:84–86.

JENKINS, D. 1961. Social behaviour in the partridge (*Perdix perdix*). Ibis 103a:155–189.

KREBS, C. J. 1985. Do changes in spacing behaviour drive population cycles in small mammals? Pp. 295–312 *in* Behavioural ecology: ecological consequences of adaptive behaviour (R. M. Sibley and R. H. Smith, eds.). Blackwell Sci. Publ., Oxford, United Kingdom.

LEFFELAAR, D. AND R. J. ROBERTSON. 1985. Nest usurpation and female competition for breeding opportunities by Tree Swallows. Wilson Bull. 97:221–224.

MacDonald, S. D. 1970. The breeding behavior of the Rock Ptarmigan. Living Bird 9: 195–238.

Martin, K. 1984. Reproductive defense priorities of male Willow Ptarmigan (*Lagopus lagopus*): enhancing mate survival or extending paternity? Behav. Ecol. Sociobiol. 16: 57–63.

Moss, R. and A. Watson. 1980. Inherent changes in the aggressive behaviour of a fluctuating Red Grouse *Lagopus lagopus scoticus* population. Ardea 68:113–119.

Olpinski, S. 1986. Breeding ecology, habitat and morphometrics of Rock Ptarmigan (*Lagopus mutus*) in Nouveau-Québec. M.S. thesis, McGill Univ., Montreal, Canada.

Petrie, M. 1986. Reproductive strategies of male and female Moorhens (*Gallinula chloropus*). Pp. 43–63 *in* Ecological aspects of social evolution: birds and mammals (D. I. Rubenstein and R. W. Wrangham, eds.). Princeton Univ. Press, Princeton, New Jersey.

Schmidt, R. K. 1988. Behavior of White-tailed Ptarmigan during the breeding season. Pp. 270–299 *in* Adaptive strategies and population ecology of northern grouse, Vol. I (A. T. Bergerud and M. W. Gratson, eds.). Univ. of Minnesota, Minneapolis, Minnesota.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman, San Francisco, California.

Wingfield, J. C. 1989. The challenge hypothesis: interrelationships of testosterone and behavior. Pp. 1685–1691 *in* Proc. XIX Int. Ornith. Congr., Vol. 14 (H. Ouellet, ed.). Ottawa, Canada.

Wittenberger, J. F. 1978. The evolution of mating systems in grouse. Condor 80:126–137.

——— and R. L. Tilson. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11:197–232.

Yasukawa, K. and W. A. Searcy. 1982. Aggression in female Red-winged Blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11:13–17.

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Comparison of activities within families and pairs of wintering Canada Geese.—Canada Geese (*Branta canadensis*) have strong family bonds and social hierarchies. Interactions within and among families of geese and dominance relationships have been described in many earlier studies (e.g., Raveling 1969, 1970; Prevett and MacInnes 1980; Lamprecht 1986; Black and Owen 1989b). Few studies have examined the effect of such social structure on the allocation of time among activities, such as foraging, resting, and vigilance. These studies usually have addressed parental investment during the breeding season (Lazarus and Inglis 1978, Giroux et al. 1986, Eberhardt et al. 1989). Most families remain intact through the winter (Elder and Elder 1949, Sherwood 1967, Raveling 1969), and adults may continue protective parental behaviors such as vigilance and defense of young. The allocation of time and energy by parental adults and their offspring in winter and the impact of parental investment on their activity budgets have not been adequately described. Extensive marking of Canada Geese in the Mississippi Flyway with neck bands (Sullivan et al. 1989) provided