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Reproductive success and survival of widowed Willow Ptarmigan hens

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The significance of male parental care and decoy behaviour for breeding success and survival of females was studied for Willow Ptarmigan *Lagopus l. lagopus*. Clutch predation and proportion of hens killed by predators after hatch did not differ for hens with and without male assistance, but widows suffered higher predation during incubation, had higher total predation, and produced fewer chicks than control hens. Only some of these differences were, however, statistically significant. The differing results between this and earlier studies might be explained by variation in male importance both between years and in differing environmental conditions, as e.g. changes in intraspesific competition and predator pressure.

Introduction

In tetraonids most species are polygynous and only five of the 17 species are monogamous (Hjorth 1970, Wiley 1974). Willow Ptarmigan *Lagopus lagopus* is normally monogamous and the males spend more time in vigilance and care of the young than males of any other tetraonid (Wittenberger 1978). Although Willow Ptarmigan usually pairs monogamously, polygyny is found to some extent. Hannon (1984) found 9% of the males to be polygynous in a population of *L. l. alexandrae* in Canada, whereas Steen et al. (1985) found 2% polygyny in a population of Norwegian Willow Ptarmigan *L. l. lagopus*. The low frequency of polygyny observed in Willow Ptarmigan has been discussed by several authors (Bergerud & Mossop 1984, Hannon 1984, Martin & Cooke 1987, Bergerud 1988).

The most general explanation for monogamy in birds is that male parental care is necessary for successful production of offspring (male parental care hypothesis) (Lack 1968, Wittenberger 1978). Here I report a test of the male parental care hypothesis by comparing the breeding success and survival of females with male assistance (the monogamous situation) and without male assistance after mid incubation (the polygynous situation).

Material and methods

The study was conducted at Gåvålia, near Kongsvold Biological Station, in central Norway (62°17′N, 09°39′E) from 1987–1989. The study area was about 10 km^2, and has been described in detail by Pedersen et al. (1983). Nests were found accidently by walking through the study area or by searching in areas near clocker droppings and lookout points of territorial cocks.

Male Willow Ptarmigan were shot for analyses of radiocesium after the Chernobyl accident, and I subsequently followed the fate of widowed hens. A total of 13 mated cocks were shot in the last part of the incubation period (1987:3, 1988:6, 1989:4) (males shot 6.5 (SE = ± 1.4) days before hatching). All hens were caught on the nest and ringed and aged as yearlings (in their second calendar year) or old, from the amount of pigment on their primaries (Bergerud et al. 1963). To assess body size and physical condition, body weight and wing length were measured (Pedersen 1988). To facilitate collecting reproductive and mortality data, all hens were equipped with necklace mounts of 12–15 g radio transmitters.

Eighteen control hens with cocks (1987:7, 1988:7, 1989:4), were found in the same area as the widows: ie. there was not a separate removal part and control part of the study area. There was no significant difference in number of widows and control hens found in different years (G-test, G = 0.91, P = 0.71, df = 2). The nests of widows were found a little earlier than the nests of control hens (widows: days before hatching: $\bar{x}$ = 14.1, SE = 1.7, n = 9; control hens: days before hatching: $\bar{x}$ = 11.7, SE = 1.6, n = 16), but not significantly so (t-test, t = 1.25, P = 0.22, df = 23). The control hens were caught, ringed, aged, measured, weighed and equipped with radio transmitters as widows. Both widows and control hens were caught during the last week of incubation (days before hatching: widows: $\bar{x}$ = 5.9, SE = 0.63, n = 9; control hens: $\bar{x}$ = 4.9, SE = 0.75, n = 14) (t-test, t = 1.26, P = 0.22, df = 21).

Predation of eggs or females was recorded through observations every 1–3 days, either by telemetry or by observing the nest through binoculars. The hens were not flushed from the nests when checked. After hatching the broods were located every two days.

Chick production was estimated as number of chicks per brood seven days after hatching. One week old chicks can be difficult to find, and to allow detection of as many chicks as possible in a brood, a tape with chick distress calls was played for two minutes after the hen was flushed. Number of chicks per brood was estimated as total number of chicks observed after flushing the hen (see Pedersen 1989). Survival of hens was recorded two weeks after hatching. The number of hens in the different analyses varies because of missing data from some hens. All statistical tests are two-tailed.

Results

Before the data from different years were combined, several reproductive and conditional variables were tested using ANOVA for annual differences in control hens. However, no significant year effect was found for either wing length (F = 0.93, P = 0.43, df = 2), body weight (F = 0.41, P = 0.67, df = 2), physical condition, measured as body weight/wing length (g/cm) (F = 0.11, P = 0.90, df = 2), clutch size (F = 1.47, P = 0.26, df = 2), date of hatch (F = 0.02, P = 0.97, df = 2), or number of hatched eggs (F = 0.67, P = 0.54, df = 2). Thus, the data from all years are combined in the further analyses.

Low sample size did not allow testing of annual differences in widows. However, the pro-

Table 1. Number of nests robbed and hens killed during incubation or two weeks after hatching in widows and control hens.

	Incubating hens		Nests		Hens with chicks		Total hens	
	Killed	Survived	Robbed	Succeeded	Killed	Survived	Killed	Survived
Widows	2	11	2	9	1	4	3	10
Controls	0	18	2	16	0	7	0	18
	G_{ran} = 3.67 P = 0.08		G_{ran} = 0.28 P = 0.66		G_{ran} = 1.88 P = 0.26		G_{ran} = 5.67 P = 0.03	

portion of widows and control hens found in different years was the same and data on widows and control hens were obtained from the same area, outruling area effects. Therefore annual differences in widows are unlikely to exist and the data from all years are combined.

Clutch predation and proportion of hens killed by predators after hatching did not differ between widowed and control hens (Table 1). However, widows suffered a higher predation than controls during incubation (15% and 0% respectively), although not significantly so. Predation of hens during incubation and after hatch combined, here called total predation, was significantly higher on widows than on controls (Table 1). The mean number of chicks per brood seven days after hatching was slightly higher in control hens than in widows ($\bar{x}$ = 6.8, SE = 1.2, n = 5 and $\bar{x}$ = 4.3, SE = 1.6, n = 4 respectively), but this difference was not statistically significant (Mann-Whitney U-test, z = 1.48, P = 0.14). Mean number of eggs hatched by control hens and widows did not differ (Table 2). However, only 5 of 14 control hens and 4 of 8 widows were used in calculating chick production, and for these hens mean number of eggs hatched was 8.4 and 10.0 respectively. This gives a survival of chicks during the first week after hatching of 81% in control hens and 43% in widows. To allow comparison of chick production between widows and control hens, the observed number of chicks per brood was multiplied by the mean brood size for the two groups divided by the mean for the group. Due to low sample sizes the adjusted chick production in widows and control hens was not significantly different (Mann-Whitney U-test, z = 1.72, P = 0.09).

The differences found in total predation of females and in chick production between widows and control hens could be caused by differences between the two groups in age ratio, body condition, and several reproductive variables (see Pedersen 1990, Hannon & Martin 1992). The data was therefore tested for such differences.

The age structure of widows and control hens did not differ: 66% of widows were yearlings and 50% of control hens were yearlings (G-test, G = 0.54, P = 0.53, df = 1). Widows were found to have the same physical condition as control hens, either expressed as body mass ($\bar{x}$ = 490.5, SE = 11.2, n = 10 and $\bar{x}$ = 492.5, SE = 6.5, n = 14 respectively) (t-tests) (t = 0.17, P = 0.87, df = 22), or when corrected for body size (body weight/wing length (g/cm) (t = 0. 48, P = 0. 64, df = 20) (Table 2). Widows were also found not to differ from control hens in either of the reproductive variables (t-tests); clutch size (t = 0.21, P = 0.84, df = 26), number of eggs hatched (t = 0.18, P = 0.86, df = 20) or date of hatch (t = 0.48, P = 0. 64, df = 23) (Table 2).

Discussion

Both lone females and lone males have been observed to raise broods (Watson & Jenkins 1964, Bergerud 1970, Miller & Watson 1978, Pedersen & Andersen 1982, Hannon 1984, Pedersen & Steen 1985, Martin & Cooke 1987). Why do not more Willow Ptarmigan become polygynous in undisturbed populations? If males can restrict their input of energy in future offspring to fertilization of the eggs, polygyny is advantageous for males (e.g. Hannon 1983, 1984). However, to

Table 2. Wing length, physical condition, clutch size, number of eggs hatched and date of hatch in widowed and control Willow Ptarmigan hens (X ± SE). [a] Body weight/wing length (g/cm), [b] 1 June is day one.

	Wing length (cm)	Physical condition[a]	Clutch size	Eggs hatched	Hatch date[b]
Widows	19.1 ± 0.11	25.7.± 0.65	9.7 ± 0.54	9.3 ± 0.53	27.7 ± 0.58
(n)	(10)	(10)	(10)	(8)	(9)
Controls	19.0 ± 0.08	26.0 ± 0.31	9.6 ± 0.98	9.1 ± 0.33	27.1 ± 0.68
(n)	(12)	(12)	(18)	(14)	(16)

become the prevalent mating system it has to be advantageous for females as well (Orians 1969).

Bergerud & Mossop (1984) explained the existence of monogamy in Willow Ptarmigan by means of a female choice model in which hens select for exclusive accompaniment by conspicuous, vigilant males. They suggested that male defence behaviour in Willow Ptarmigan is important for the reproductive success of females because it deflects predators away from females during nest search, egg laying and incubation, and from hens with chicks. In two studies, where males were removed at various times during the breeding season (Hannon 1984, Martin & Cooke 1987, Hannon & Martin 1992), there has been found that male accompaniment did not influence reproductive success or survival of females. This suggests that male parental care and decoy behaviour is not essential to females and the male parental care hypothesis was rejected.

The differences found in hen survival and chick production between widows and control hens were not due to effects of age, physical conditions, clutch size or number of eggs hatched. The results therefore suggest that male presence, which normally includes parental care and decoy behaviour, is important for chick and hen survival. Also in an earlier study in the same population, Pedersen & Steen (1985) found that lone females had slightly smaller broods, although not significantly so, than accompanied females, indicating that male parental care is important for chick survival. Although the material is limited and differences in chick production are not statistically significant these results support the hypothesis of Bergerud & Mossop (1984).

Neither in this study nor in the study of Martin & Cooke (1987) was there any difference in clutch predation between widows and pairs. Possibly male decoy behaviour is less important in nest defence because females rely primarily on their camouflage. If the nest is found by egg predators such as Hooded Crow *Corvus c. cornix,* Stoat *Mustela erminea,* Pine Marten *Martes martes*, or Red Fox *Vulpes vulpes*, the defence of the nest, whether by a pair or a single bird, is often unsuccessful. Although the cock might be important in detecting predators and warning the hen during incubation, male antipredator behaviour deflecting predators from both the hen and the chicks might be even more important after hatching.

The potential difference between Willow Ptarmigan populations might be due to variation in the importance of male antipredator behaviour between years and in differing environmental conditions. As the ultimate goal is to recruit the offspring into the breeding part of the population, parental care, as e.g. antipredator behaviour, can be expected to change among years due to changes in competition or predator pressure (Moss & Watson 1985, Sonerud 1988 (see also Carlise 1982)). Such changes in male importance have also been suggested in House Wrens *Troglodytes aedon* (Bart & Tornes 1989) and Snow Buntings *Plectrophenax nivalis* (Lyon et al. 1987).

As suggested by Martin & Cooke (1987) the males might accompany the broods as a "salvage strategy" in case the hen is killed. Gruys (1991) found that hens with broods suffered high mortality due to raptors in the autumn, and males can raise the brood alone to avoid total reproductive failure (Pedersen & Andersen 1982). Although Hannon & Martin (1992) did not find any difference in recruitment of chicks from monogamous and polygynous hens, natal philopatry is low and their sample size was small. The importance of male assistance during the period from post-fleding to brood break-up thus remains unsolved. The "salvage strategy hypothesis" therefore remains to be tested through examining mortality of hens and chicks during this period.

To elucidate the importance of male parental care and decoy behaviour in the maintenance of monogamy in Willow Ptarmigan, as well as other precocial species, more experiments both over several years as well as during each period of the breeding season are needed.

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Selostus: **Yksinäisten riekkonaaraiden pesimismenestys**

Kirjoittaja tutki riekkokoiraan merkitystä poikasten hoidossa ja petojen harhauttamisessa.

Yksinäiset naaraat joutuivat useammin petojen saaliiksi kuin naaraat, joiden koiras avusti niitä. Yksinäiset naaraat tuottivat vähemmän poikasia kuin kontrollinaaraat. Erot eivät kuitenkaan olleet tilastollisesti merkitseviä. Koiraan merkitys poikueen hoidossa vaihdellee eri vuosina ja eri ympäristöissä, mahdollisesti lajin sisäisen kilpailun ja saalistuspaineen vaihtelujen vuoksi.

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