

The effect of manipulated brood size on parental defence in a precocial bird, the Willow Ptarmigan

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Offspring number was manipulated in Willow Ptarmigan *Lagopus lagopus* to determine the effect of brood size on parental effort in defence of young. Three chicks were added ($n = 8$), exchanged ($n = 10$) or removed ($n = 12$) among broods of females that had laid 7–9 eggs. If parents based effort on the value of the brood, it was predicted that defence should increase with offspring number because ptarmigan parents receive greater returns from large broods. Parental effort in defence was unaffected by brood size, probably because a predator cannot threaten the entire brood simultaneously when ptarmigan young are scattered. This evidence supports theoretical models which predict that if the young are able to disperse, patterns of defence will be different in precocial birds from that in fish or altricial birds.

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The theory of life history evolution is based on the premise that parents should adjust parental effort to optimize their overall benefit from current and future reproductive output (Trivers 1972, Sargent and Gross 1985). Offspring number is one of the most important factors that affects the value of current reproductive output (Clutton-Brock 1991), but the form of parental care may determine whether parental effort is influenced by offspring number. Altricial birds provide their young with food; a form of parental care that is depreciable if the benefit per offspring declines with offspring number, although total parental effort may increase (Lazarus and Inglis 1986, Clutton-Brock 1991). In precocial birds, the main components of parental care are defence, brooding and vigilance: all of which are non-depreciable forms of parental care if the benefit per offspring does not decline with offspring number. If parental care is non-depreciable, the relationship between total parental effort and offspring number can be unclear (Schindler and Lamprecht 1987).

Theoretical models (Andersson et al. 1980, Lazarus and Inglis 1986) suggest that the dispersion of young can affect the relationship between parental effort and offspring number. Lazarus and Inglis (1986) predict that parental effort should covary with offspring number if a

predator can simultaneously threaten all of the young (brood loss model, e.g. altricial young in a nest), but should be independent of offspring number if a predator is limited to taking fewer offspring because the young are scattered (fixed loss model, e.g. a brood of precocial young).

The value of a brood should increase with offspring number (Coleman et al. 1985, Sargent and Gross 1985) if the number of recruits is positively correlated with brood size (cf. Wiklund 1990) and parental effort should thus be greatest for large broods. However, parental effort and natural brood size could covary positively if parents that produce more young are also capable of providing more care, as a function of either parental ability or territory quality. Alternatively, defence may covary negatively with natural brood size if a small brood represents a greater proportion of the lifetime reproductive success of a poor quality parent than a large brood does for a good quality parent (Montgomerie and Weatherhead 1988). Experimental manipulation of offspring number is necessary to resolve whether parents adjust their effort to brood size.

Parental effort can be measured in several ways, including predation risk incurred through defence of off-

spring (Winkler and Wilkinson 1988). Defence of young has two features that make it a less ambiguous measure of parental effort than other forms of parental care. First, a parent cannot defer defence but must give an immediate response if the young are threatened. Further, inappropriate defence has a large cost: the young may be eaten by a predator if defence is weak (Montgomerie and Weatherhead 1988), but a parent can be killed if its response is strong (e.g. Brunton 1986).

This is the first study that has used brood size manipulation to examine the parental defence of a precocial bird. I examined parental defence in Willow Ptarmigan *Lagopus lagopus*, a precocial bird with nidifugous, self-feeding young. Pedersen (1989) used prolactin implants to induce strong defence in Willow Ptarmigan, and found that manipulated females fledged more young. I performed a complementary experiment in this study: I manipulated offspring number to determine whether ptarmigan adjust parental effort in defence to changes in brood size. I predicted that if ptarmigan adjust effort to the value of a brood, defence should covary with brood size since more recruits return from larger broods (Martin and Hannon 1987).

Methods

Willow Ptarmigan were studied at Chilkat Pass, in north-western British Columbia, Canada (59°50'N, 136°30'W) during the breeding seasons of 1989, 1990 and 1992. The study area and general methodology are described elsewhere (Martin et al. 1989). Willow Ptarmigan are a monogamous, ground-nesting grouse with a circumpolar distribution. In Chilkat Pass, females lay clutches of 5–11 eggs (Martin et al. 1989), and intraspecific nest parasitism is rare (Sandercock 1993). Willow Ptarmigan can renest if their first nest is destroyed during laying or early incubation (Parker 1981, Robb et al. 1992), but only broods from first nests were used in this study.

The young of Willow Ptarmigan are self-feeding, and brooded regularly by the female until they are able to maintain homeothermy at about 6 days of age (Aulie 1976). Willow Ptarmigan are unique among grouse because the male remains with the female to defend the young after hatch (Wittenberger 1978). Natural encounters between predators and grouse nests or broods are only rarely observed (Martin 1985, Hik et al. 1986, Sone-rud 1988), but potential predators of ptarmigan young at Chilkat Pass include: red foxes *Vulpes vulpes*, short-tailed weasels *Mustela erminea*, Northern Harriers *Circus cyaneus*, and Short-eared Owls *Asio flammeus*.

Willow Ptarmigan were captured on breeding territories before laying began, and classed as 1-year olds or adults by comparing pigmentation patterns on the primary wing feathers (Bergerud et al. 1963). Each bird was uniquely colour-banded and females were radio-marked to facilitate finding nests and broods. Each female was

flushed from the nest to estimate the day of hatch and clutch size: once when the nest was first found, and once after laying was completed. In some cases, the eggs were floated in water (after Westerkov 1956) to estimate stage of incubation. Date of first egg was calculated by back-dating, assuming a laying rate of one egg per day and that incubation began on the penultimate egg (Sandercock 1993). At hatch, all chicks were individually marked with patagial wing tags (Hannon et al. 1990). Radio-marking (Schieck 1988) and wing-tagging (Hannon et al. 1990) do not influence either reproductive success or survival.

Brood size manipulation

I controlled for parental quality in this study by including only females that had laid clutches of 7–9 eggs. Birds were randomly assigned to treatments, and brood size was manipulated on the day of hatch. Three chicks were added to *addition* broods ($n = 8$, $\text{mean} \pm 1\text{SD} = 11.0 \pm 0.9$ chicks), and three chicks were removed from *removal* broods ($n = 12$, 4.9 ± 1.0 chicks). The size of manipulated broods (4–12 chicks) was similar to the range in size of natural broods (5–11 chicks, Martin et al. 1989). To control for manipulation disturbances, I exchanged three chicks between *control* broods ($n = 10$, 8.2 ± 0.8 chicks). Infertile eggs that failed to hatch were counted as if a chick had been moved in removal broods, and not replaced in control or addition broods.

Measurement of parental defence

Defence by the female and male was recorded the day after the brood size manipulation. The chicks were one day old, and the parents had about 24 hours to adjust to the change in brood size. This has been shown to be an adequate period for acclimation in several studies that have manipulated the brood size of birds (Knight and Temple 1986, Windt and Curio 1986, Wiklund 1990). Defence was recorded once to avoid habituation and because brood size could change through attrition. Unaccompanied females were included because male presence does not affect female defence (Pedersen and Steen 1985, Sandercock 1991). Three of the five males that were absent when defence was recorded were later observed attending the brood.

The broods were located by radio-telemetry, and two observers approached until a parent reacted. One observer recorded female behaviour, and the other observer recorded male behaviour for three minutes in response to playback of a day old chick's distress call from a hand-held tape recorder. Distress calls differ in pitch from contact calls (Wike and Steen 1987), and are used when the young are threatened.

Willow Ptarmigan defence contains elements of both distraction and aggression, and these behaviours could not be distinguished during an encounter because they

Table 1. Brood success of Willow Ptarmigan in the experimental treatments. Offspring number was manipulated by adjusting brood size at hatch by three chicks.

Treatment	Total brood loss ^a		Success of broods where at least one young fledged					
	%	n	Brood size at fledging			Percent of brood surviving		
			\bar{x}	SE	n	\bar{x}	SE	n
Addition	25.0	8	4.50	0.85	6	40.3	6.7	6
Control	12.5	8	5.14	0.67	7	61.0	7.3	7
Removal	18.1	11	2.56	0.38	9	52.4	9.1	9
G	0.30							
H ^b			2.75					
P	0.86		0.25					

^a Sample size differs from Fig. 1 because 2 radio-collars failed, and because one female was killed by a fox 8 days after hatch.

^b Kruskal-Wallis test.

often intergraded. Three types of behaviour were considered to be defensive and were recorded in the focal observations: postures, vocalizations and distance. Active postures (including running, wing dragging, shaking plumage, short active flights) and vocalizations were an indication of the parents' state of agitation, and could affect their reaction time and exposure to a predator. Distance from the observer was considered a good measure of a parent's aggression because a bird within a predator's striking distance would be at risk. Defence intensity was strongest at the start of the encounters, although particularly aggressive parents continued to defend after the young had scattered. Parents reacted as if the observers were a threat to their young, because parents with young were obviously more defensive than birds without broods.

Estimating brood survival

Broods were followed for two weeks after hatch. Counts of brood size were used to estimate the minimum number of chicks that were present when defence was recorded. The estimate of chick survival is conservative because in any count, some chicks could have been present but hidden, and subsequently died before being resighted again. Willow Ptarmigan chicks are nourished by an invaginated yolk sac until 2–3 days of age (Bergerud 1970), and chick survival was expected to be high initially. In 1990 and 1992, I made concerted efforts to recapture young during brood-rearing, and to determine the fate of the chicks fostered to other broods. Brood success was estimated when the young were 9–14 days of age and starting to fly. The broods were flushed several times in this period, and the highest count was taken as the best estimate of brood size at fledging.

Results

Rates of depredation on first nests were high in 1989 (66.7%, $n = 42$), 1990 (77.3%, $n = 88$), and 1992 (77.3%, $n = 44$), and reduced the number of broods available for manipulation. I pooled years because Willow Ptarmigan defence is unaffected by annual conditions at Chilkat Pass (Sandercock 1991), and because the sample of broods was small.

Chick survival until defence was recorded

Broods would have changed treatment group in the experiment if three or more chicks died before defence was recorded. From subsequent brood counts, I determined that only 16.7% ($n = 30$) of the broods could have lost three or more chicks before defence was recorded, indicating that chick survival was good. Chick loss was evenly distributed among treatments. The counts of brood size underestimate survival because chicks are easily overlooked, and hence actual survival was probably even better.

Chicks that were moved to foster broods at hatch in 1989 (22.3%, $n = 103$), 1990, (18.4% $n = 152$), or 1992 (12.7% $n = 71$) could have had low survival if parents neglected unfamiliar young. The proportion of fostered young recaptured among chicks and fledglings (Binomial test, 1990 23.1% $n = 26$, $P = 0.15$; 1992 18.6% $n = 43$, $P = 0.08$), or recaptured among 1-year olds the following year (1989 33.3% $n = 9$, $P = 0.21$; 1990 0% $n = 7$, $P = 0.24$) was not significantly different from the proportion of fostered young in the sample of chicks that were tagged at hatch. The result does not change if survival is calculated on a per brood basis.

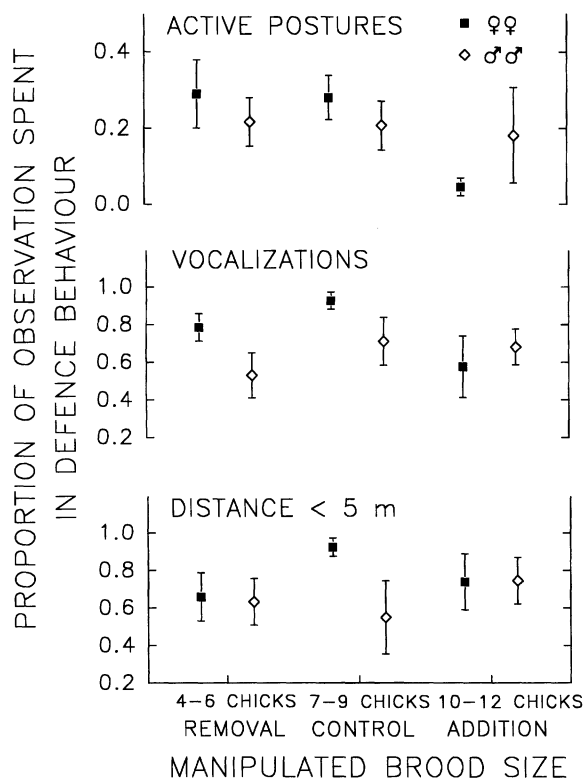


Fig. 1. The proportion of the encounter that the parent spent in defence behaviour as a function of manipulated brood size (removal $n = 12$, control $n = 10$, addition $n = 8$). All females had initial clutches of 7–9 eggs, and manipulated brood size ranged from 4–12 chicks. Defence was recorded when the young were one day old. Means are shown \pm 1SE.

The effect of manipulated brood size on brood success and parental defence

There was no significant difference among parents in the experimental treatments in age class (♀ ♀ mean = 60% 1-year olds, $G = 0.013$, $P = 0.99$; ♂ ♂ mean = 33% 1-year olds, $G = 0.31$, $P = 0.85$) or adjusted (after Robb et al. 1992) body condition (B.K. Sandercock unpubl. data, ♀ ♀ $F = 0.95$, $P = 0.40$; ♂ ♂ $F = 0.26$, $P = 0.78$). Further, there was no significant difference among treatments in the rate of total brood loss, or the percentage of the brood that survived until fledging (Table 1). All cases of total brood loss were caused by gradual attrition of young during brood-rearing, and not by sudden failure. The estimates of brood survival were unaffected by the number of times the brood was flushed after fledging ($H = 1.96$, $P = 0.38$).

I have reported estimates of slope based on the untransformed data below because the conclusions were unchanged whether untransformed proportions (p) or the arcsin \sqrt{p} were used in the regression (Model I) analyses. There was no significant trend across treatments (Fig. 1, $df = 1$ all tests) in the time that males spent in active postures ($b = -0.02$, $F = 0.09$, $P = 0.77$), or the time

that females and males spent vocalizing (♀ ♀ $b = -0.09$, $F = 1.52$, $P = 0.23$; ♂ ♂ $b = 0.10$, $F = 1.56$, $P = 0.22$) or less than 5 m from the observer (♀ ♀ $b = 0.06$, $F = 0.42$, $P = 0.52$; ♂ ♂ $b = 0.02$, $F = 0.03$, $P = 0.87$). There was a marginally significant negative trend across treatments in the time that females spent in active postures ($b = -0.11$, $F = 4.83$, $P = 0.04$). Addition females spent the least amount of time in active postures (Fig. 1), contrary to the prediction that defence should increase with brood size.

Discussion

The survival of young until fledging was independent of adjusted brood size in Willow Ptarmigan, as it is in ducks (Rohwer 1985, Eadie 1989), and geese (Lessells 1986). This evidence, and the occasional brood mixing that is observed in grouse (Keppie 1977, Maxson 1978), supports the assumption that parental care in precocial birds is generally non-depreciable. Semipalmated Sandpipers *Calidris pusilla* are the only precocial bird where enlarged broods have been reported to have lower survival (Safrieli 1975). Shorebirds may have more difficulty brooding extra young because they use a pair of brood patches (Wiebe and Bortolotti 1993) to incubate a clutch of four eggs (Maclean 1972), whereas waterfowl and grouse use one large brood patch to incubate or brood a variable number of young (Winkler and Walters 1983).

The relationship between parental effort and brood size is unclear if parental care is non-depreciable. For example, time spent in vigilant behaviour or brooding increases with natural brood size in some (Walters 1982, Erikstad and Andersen 1983, Schindler and Lamprecht 1987), but not all (Lazarus and Inglis 1978, Walters 1982, Lessells 1987) precocial birds. Similarly, parental defence is positively correlated with natural clutch or brood size in some fish (Pressley 1981, but see Lachance and Fitzgerald 1992) and birds (Gottfried 1979, Curio and Regelmann 1987, Wallin 1987, Wiklund 1990; including Willow Ptarmigan, Pedersen and Steen 1985, Hudson and Newborn 1990, but see Martin and Horn 1993), but not others (Breitwisch 1988, Hobson et al. 1988). Unfortunately, comparisons of defence and natural brood size reveal little about whether parents adjust parental effort to offspring number, and experimental manipulation of brood size is necessary to demonstrate whether parents adjust parental effort.

Studies that have manipulated clutch or brood size in fish (Sargent 1981 in Clutton-Brock 1991, Carlisle 1985, Coleman et al. 1985, Ridgway 1989, Lavery and Keenleyside 1990) and altricial birds (Robertson and Biermann 1979, Greig-Smith 1980, Knight and Temple 1986, Windt and Curio 1986, Wiklund 1990) have consistently reported that defence is correlated positively with the adjusted number of offspring. There is one exception: Winkler (1991) showed that reduced brood size had no

effect on the defence in Tree Swallows *Tachycineta bicolor*, and that nest abandonment was a better indicator of parental investment decisions. Willow Ptarmigan do not have the option of abandoning their young to produce another brood because they can only replace clutches that are lost early in incubation (Parker 1981, Robb et al. 1992).

Parental defence was unaffected by adjusted brood size in this study, and Willow Ptarmigan appear to be an exception to previous experimental studies. Number of young at hatch and at fledging are uncorrelated positively (Spearman $r = 0.51$, $P < 0.001$) in unmanipulated broods at Chilkat Pass (1985–1990, $n = 77$), and more recruits return from large broods of fledged chicks (Martin and Hannon 1987). The survival of fostered young indicates that parents were unable to recognize or did not discriminate against unfamiliar chicks. Defence was unaffected by brood size in Willow Ptarmigan even though the value of the brood increases with offspring number.

Lazarus and Inglis (1986) predicted that dispersion of young can affect the relationship between parental effort and offspring number. If a predator can simultaneously threaten all of the young (brood loss model, Lazarus and Inglis 1986), defence should covary with number of offspring. In the previously mentioned studies that manipulated clutch or brood size in fish and altricial birds, parents defended offspring that were clumped in a nest. Carlisle (1985) did not describe the behaviour of cichlid broods, but cichlid fry usually school together when threatened (Keenleyside 1979). Defence may covary positively with brood size in fish and altricial birds because a predator can take the entire brood in a predation event.

In contrast, young of Willow Ptarmigan disperse quickly when threatened, and parents direct defence towards the predator while the cryptic young are concealed. Foxes are attracted to defence by grouse (pers. obs.), and can use defence as a cue to perform an area-concentrated search for young (Sonerud 1988). Presumably, the number of young taken by a predator could increase with brood size in this case. However, because precocial young are effective at scattering to hide, the profitability of searching may decline independently of brood size, and well before the entire brood is consumed. Sonerud's (1988) observations of two encounters support this suggestion; the fox he observed found only 1–2 chicks per brood, and abandoned searching after about 30 min. Hence, defence may be unaffected by brood size in Willow Ptarmigan because a predator cannot threaten the entire brood but must search for each of the scattered young (fixed loss model, Lazarus and Inglis 1986).

In this study, the first attempt to use a brood size manipulation to examine the parental defence of a precocial bird, I provide some initial empirical evidence to support theoretical models that predict that the ability of young to disperse should produce different patterns of defence in altricial and precocial birds. Further manipulations of brood size in shorebirds, waterfowl and other grouse are required before brood size-independent de-

fence can be accepted as a general pattern of parental investment in precocial birds.

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