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Changes in the numbers and interspecific interactions of Red Grouse *(Lagopus lagopus scoticus)* and Black Grouse *(Tetrao tetrix)*

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Abstract — Numbers of Red Grouse *Lagopus lagopus scoticus* and Black Grouse *Tetrao tetrix* fluctuated over the years on three Scottish moors where both lived. Black Grouse tended to peak in numbers at, or one or two years after, a trough in Red Grouse numbers. During interspecific disputes in the wild and in captivity, the smaller Red Grouse usually dominated the Black Grouse. We discuss the possibility that Red Grouse at high densities depress Black Grouse numbers on moorland through aggressive competition, and speculate whether such interactions have adaptive value.

Introduction

Inverse relationships between densities of closely-related species are often explained as results of interspecific competition. This generalization, fundamental to avian community ecology, has been based largely on patterns observed in short-term comparative studies of multi-species assemblages, and short-term experiments. Wiens (1989) recommended that a long-term perspective might provide additional insights into the processes involved. Here, we present long-term data on densities of two related species, Red Grouse *Lagopus lagopus scoticus* and Black Grouse *Tetrao tetrix,* on three moors in north-east Scotland.

At two of the moors, we noticed some interspecific interactions between Red and Black Grouse in which the smaller Red Grouse usually dominated. This was unexpected since bigger species usually dominate small ones (eg Willow Ptarmigan *Lagopus lagopus* dominated Rock Ptarmigan *Lagopus mutus* (Moss 1972)). Such aggression between the two species suggested that there might be interspecific competition. We therefore compared the numbers of Red and Black Grouse to see if there was an inverse relationship. To check the pattern of disputes further, we made experimental observations of aggressive interactions between the two species in captivity.

Study areas and methods

Wild birds

All three study areas were on moorland dominated by heather *Calluna vulgaris.* Glen Esk (460 ha) comprised the 'low' study area of Jenkins *et al.* (1963) and Kerloch the 'intensive' study area (177 ha) of Watson *et al.* (1984). At Rickarton, experimental manipulation of part of the Red Grouse population was followed by a difference in their densities between experimental (north, 202 ha) and control (south, 243 ha) areas (Watson *et al.* 1988) and so data from each are presented separately here. Glen Esk, Kerloch and Rickarton lay respectively 39 km south-west, 21 km south-west and 11 km south-east of Aberdeen. Red and Black Grouse were counted as described by Jenkins *et al.* (1963), Watson and Miller (1976) and Parr and Watson (1988).

The areas were originally chosen for studying Red Grouse, which lived for much of the winter and spring on relatively small territories (Watson and Miller 1971) almost entirely on the heather moorland. Black Grouse, however, used woodland as well as heather moorland and had much bigger home ranges than Red Grouse (e.g. 303-689 ha for individual Black Grouse in Glen Dye, 6 km west of Kerloch (Robel 1969)). Therefore, it was reasonable to regard the Red Grouse on each area as a population for demographic purposes (Jenkins *et al.* 1963, Watson *et al.* 1984, Watson *et al.* 1988). Although some Black Grouse did breed and rear young on the study areas, it is probable that many of the birds we studied spent relatively more time off the areas than Red Grouse, and we claim only to describe their use of our moorland study areas.

Captive birds

Captive birds used in the experiments were reared as in Moss *et al.* (1981). The Black Grouse comprised our entire stock of captives, whereas the

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Red Grouse were birds, more than one year old, selected at random from stock. Interactions were studied in spring when the hens of both species were about to, or had just started to, lay and cocks were displaying intensely. The aim was to find if one species usually dominated the other. Since dominance can be site-specific, the ideal was to study interactions between birds which were showing territorial behaviour on the boundaries of their own territories. However, because of the different social organization of the two species, it was difficult to replicate in captivity the circumstances of natural encounters.
In the wild, individual Blackcocks (Black Grouse cocks) defend territories which can be as small as a few m^2 (Cramp 1980) on a communal display area (a lek) which forms a tiny proportion of their home range. In captivity they established realistic territories with defended boundaries in a large sectional run with small sliding doors in each intemal partition (Fig. 1). Red Grouse, on the other hand, have a territorial social system and defend territories typically of several ha in the wild (Watson and Miller 1971), a size which it is not practicable to provide in captivity. Nevertheless, cocks do show typical territorial displays along the boundaries of small, enclosed runs in captivity. We could therefore have an experimental layout which simulated the intrusion of territorial Red Grouse on to a Black Grouse lek.

S	S	OR	RG	GR	GR	GR	RG	MR	MR	S
	OR	OR	OR	OR	RG	MR	MR	MR	MR	S

Figure 1 - Experimental run layout in 1988. _____ solid partitions (sliding doors shut except during bouts); — — — — — — — partitions with open doors; S subordonate Blackcock; GR, OR and MR territorial Blackcocks; RG Red Grouse.

The two experiments (1987 and 1988) were each done in four stages. First, in late March to early April eight or nine Greyhens (Black Grouse hens) were released into the run (Fig. 1), with all the sliding doors open. Second, two days later, seven or eight Blackcocks were introduced. The Greyhens coexisted with few aggressive interactions throughout either experiment, but the Blackcocks fought and chased each other vigorously during the first few days, until (in each experiment) three cocks had established territories and were displaying frequently. The remaining cocks were clearly subordinate, did not display during this initial period, avoided or hid from the territorial cocks and in some cases had feathers missing from their napes following beatings. In 1987, one subordinate cock lived peaceably within the territory of one of the territorial cocks. In both years, other subordinate cocks were shut off in separate sections of the run to avoid unnecessary stress. Once they had been shut off, the subordinate cocks did eventually begin to display.
Stage three, in mid-April, involved introducing three Red Grouse cocks (1987) or pairs (1988) into single sections of run, within the Blackcock territories but shut off by closed doors. The Red Grouse cocks soon showed territorial behaviour and displayed mutually with Blackcocks along the partitions. Both species frequently showed "walking-in-line" displays (Watson and Jenkins 1964, Cramp 1980) and attempted to peck and to beat each other with their wings. In stage four (late April to early May), the door separating one of the Red from the Black Grouse was opened and interactions recorded from a tower hide. When one or more decisive encounters had occurred (usually in less than an hour), the Red Grouse was again shut off in his run. This was done for each Red Grouse on 1-3 occasions. To check dominance relationships between Red Grouse, two sliding doors were opened. When this was done, the Red Grouse usually disputed with each other and largely ignored the Black Grouse.

Results

Numbers of wild birds

Fluctuations in numbers of Red Grouse often show non-random, cyclic patterns (Watson and Moss 1979, 1980) with periods of increase following periods of decline (Fig. 2). At Glen Esk, Kerloch and Rickarton, Black Grouse, when they occurred, tended to peak in numbers at, or one or two years after, a trough in Red Grouse numbers (Fig. 2). This happened in 1961 at Glen Esk, in 1965 and 1971 at Kerloch, in 1981 at Rickarton south and possibly in 1980 at Rickarton north. The peak in Black Grouse numbers at Rickarton south in 1985, however, did not fit this generalization. More precisely, when present on Red Grouse study areas, Black Grouse tended to (i) increase during cyclic-type declines of Red Grouse and also (ii) to increase during the early stages of cyclic-type increases, but then (iii) declined as Red Grouse increased towards peak densities.
Overall, 23 out of 27 observed annual changes in Black Grouse numbers fitted this pattern ($P < 0.001$ by a binomial test). Three of the four years data which did not fit the generalization were at Rickarton south in 1985-88. Red Grouse densities were generally lower at Rickarton than at Glen Esk and Kerloch, and so the same relationships between Red and Black Grouse might not have been expected. If data from Rickarton are excluded, then 15 out of 16 changes in Black Grouse numbers fitted the above generalization ($P < 0.001$, binomial test). At Glen Esk (1958-62) and Kerloch (1966-73) the

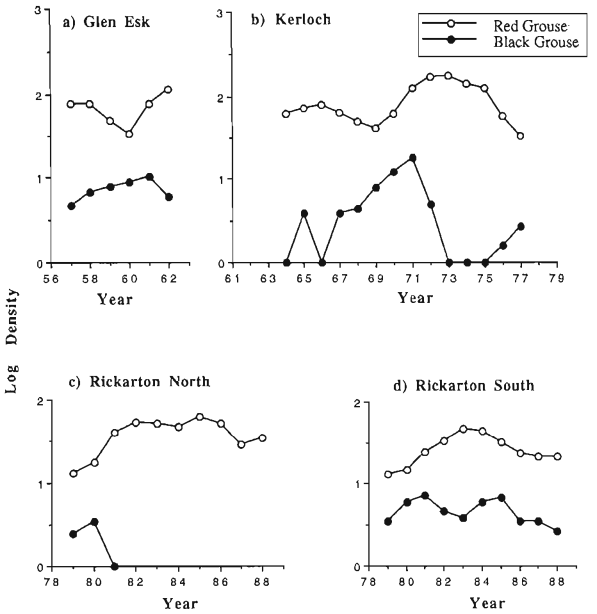

Figure 2 - Densities (birds/km^2 in spring) of Red (log D) and Black (log D+1) Grouse at a) Glen Esk, b) Kerlock, c) Rickarton north and d) Rickarton south.

relationships between Black Grouse densities in spring t (B_t) and Red Grouse densities in spring t - 1 (B_{t-1}) were very similar:

Glen Esk $B_t = 11.53 - 0.069R_{t-1}$ ($R^2 = 0.71$)
Kerloch $B_t = 11.67 - 0.046R_{t-1}$ ($R^2 = 0.33$)

Although the above regressions were not significant separately (two-tailed $P = 0.072$ and 0.169 respectively) their similarity made it reasonable to apply a one-tailed probability estimate to the second result (Kerloch, $P = 0.085$) and then to combine the two probabilities according to $\chi^2_4 = -2 \Sigma \log_e P = 10.19$, (combined $P<0.05$). This indicated a delayed density-dependent relationship in which Black Grouse densities tended to follow Red Grouse densities with a lag of one year. No simple inverse correlation between B_t and R_t was observed.

Behavioural interactions between species

Interspecific disputes between wild Black and Red Grouse (Appendix I) were seen in years of high Black Grouse numbers at Glen Esk, and in years when numbers were increasing at Kerloch. Cock Red Grouse dominated Blackcocks and Greyhens in 11 out of 12 encounters. No interactions involving Red Grouse hens were seen.

In captivity, the territorial Blackcocks were two or three years old while the subordinate cocks were one (young), two and four years old (Table 1). This dominance over young by old cocks is also observed in wild Black Grouse (Johnstone 1969) but not in Red Grouse, either in the wild (Watson and Miller 1971) or in captivity (Moss et al. 1984). Therefore, the fact that the Red Grouse were all old birds (two or three years) would have had no bearing on the results of the experiment.

Table 1 - Status and age in years of captive Blackcocks.

	1987			1988		
	Bird	Territory*	Age	Bird	Territory	Age
Territorial	PR	7	3	MR	6	2
	GR	6	2	GR	3	3
	OR	2	2	OR	5	3
Non-territorial	ML	—	1	ML	—	2
	BR	—	1	BR	—	2
	MR	—	1	PR	—	4
	NR	—	1	OL	—	1

* Number of sections defended.

The results from the two years were broadly similar (Table 2). Of the seven dyadic Red-Black Grouse relationships studied in 1987, six involved "away" wins by Red Grouse on Black Grouse territories, with one draw at a boundary door. The Red Grouse cock involved in the draw had been dominated by both the other Red Grouse in interactions following the opening of two sliding doors. In 1988, all five Red-Black Grouse dyadic relationships observed involved dominant Red Grouse on Black Grouse territory.

Since the Blackcocks involved in these encounters all dominated the non-territorial Blackcocks, it is reasonable to infer that the Red Grouse would also have dominated the latter. If one assumes a linear hierarchy involving both species (including the subordinate Blackcocks), the results for 1987 and 1988 were: Mann-Whitney $U_{3,7} = 0$, $P = 0.008$; and $U_{3,8} = 0$, $P = 0.002$.

In addition, there were 11 interactions involving Red Grouse cocks (four individuals) and Greyhens (eight individuals); and three interactions involving one Red Grouse hen and three Greyhens. In each case, the Red Grouse were dominant.

Discussion

One of the patterns often used to infer interspecific competition between closely related species is an inverse relationship in densities. The present work provides an example of this, but with low Black Grouse numbers tending to lag a year behind high

Table 2 - The results of disputes between captive Red and Black Grouse in 1987 and 1988.

Year	Red Grouse	Black Grouse		
		GR	PR	OR
1987	A	chase	draw*	—
	B	chase/peck**	chase/peck	chase/peck
	C	—	chase/peck	chase/peck (2)
		GR	MR	OR
1988	D	chase (2)	chase/peck	
		chase/peck (2)	peck/retreat	—
			retreat	—
	E	—	—	chase (4)
				chase/peck
				peck
	F	—	retreat/peck (2)	—

(n) number of encounters of this type if>1.

Red Grouse dominated (except*) Black Grouse inside Black Grouse territories except (**) which was inside a Red Grouse territory. Black Grouse retreated. No reverse situation were observed during the experiments.

Red Grouse densities. This lag could occur if Red Grouse tend to inhibit young Black Grouse recruits from settling on an area, while having little effect on established adults. Peaks in shooting bags of Red and Black Grouse in Scotland have usually occurred within 2-3 years of one another (MacKenzie 1952). However, peaks in bags of Black Grouse have tended to come before those of Red Grouse (MacKenzie 1952), which is consistent with the suggestion that Red Grouse at high densities may reduce numbers of Black Grouse.

Wiens (1989) emphasised that inverse relationships between the densities of different species may be due to various processes and need not involve competition. For example, some aspect of the environment may change to the relative advantage of one species and the detriment of another. Certainly, Black Grouse on heather moors are generally found where the heather is on average taller than where high densities of Red Grouse occur (Parr and Watson 1988). However, the changes in numbers of both species in the present study were much too rapid to be explained by changes in the heather sward.

In the wild, Red Grouse are on their territories while Black Grouse are away from their display grounds. This idea is reinforced by the fact that the more closely matched encounters between Red and Black Grouse (Appendix I, (iv)) were observed in a field near a Blackcock lek. This was not so in captivity, however, where the mechanism seemed to be that Red Grouse were readier to attack and were better fighters. This relationship is consistent with the observations that Black Grouse densities tended to decline at high Red Grouse densities, but not vice versa, and allows one to postulate that aggressive interactions contributed to declines.

Interspecific aggression, however, does not necessarily imply competition as usually understood in the context of avian community ecology. Most definitions of competition also imply limitation of shared resources as a precondition of competition. This might be the case here, as heather is the main food of Red Grouse (Watson and Miller 1976), and is also one of the main foods of Black Grouse in Scotland (Johnstone 1969). The evidence suggests that "exploitation" competition is unlikely, but "interference" competition remains a possibility. It is possible that excluding Black Grouse from part of their range will reduce their performance.

Discussions of competition often involve assumptions that the birds' behaviour is in some sense optimal. It could be that driving Greyhens off the moor in spring, when good nutrition is critical (Moss 1977), allows Red Grouse hens greater access to the best food.

Alternatively, the Red Grouse cocks' aggression might in some way enhance their social status and consequent access to resources and mates. More plausible, perhaps, is the suggestion (Murray 1971, 1976) that this behaviour is largely a consequence of misdirected aggression towards individuals of other species that are similar in behaviour. Certainly, some behaviour by tetraonids seems misdirected. Cock Capercaillie *Tetrao urogallus* sometimes attack humans, cock Willow Ptarmigan court Rock Ptarmigan hens (Moss 1972) and in the present study captive cock Red Grouse courted Greyhens. Relevant to this is the suggestion by Cramp (1980) that Black Grouse may interbreed with Red Grouse, Capercaillie and Pheasant *Phasianus colchicus*, and Capercallie with pheasant. In captivity, we have found that Red Grouse will interbreed with Rock Ptarmigan producing viable offspring.

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Riassunto — Il numero di Pernici bianche di Scozia e di Galli forcelli, in tre aree simpatriche di brughiera della Scozia, varia notevolmente di anno in anno. I Galli forcelli raggiungono i massimi numerici in corrispondenza dei minimi nella Pernice bianca di Scozia, o uno-due anni dopo. Durante interazioni competitive sia in campo che in aree recintate, la Pernice, più piccola, normalmente domina sul Gallo Forcello, più grosso. Si discute l'eventualità che la Pernice bianca di Scozia, ad alta densità, deprima la popolazione di Forcelli attraverso competizione aggressiva e del possibile ruolo adattativo di tali comportamenti.

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Appendix I

Disputes between Red and Black Grouse

At Kerloch we noted interspecific disputes between Red and Black Grouse on seven out of 32 occasions when they were within 5 m of each other; all seven were in 1968-71 when both species were increasing. Three encounters at Glen Esk were in 1961 and two in 1986, both years of high Black Grouse numbers there. All Red Grouse involved were cocks, which dominated in all encounters but one.

(i) Threat, once. - A Red Grouse raised his head and combs when a Blackcock walked within 4 m.

(ii) Short encounter, four times. - (a) A Red Grouse with stretched neck and raised combs, and a Blackcock with fanned tail faced each other 2 m apart. After half a minute the Blackcock broke off. (b) A Red Grouse gave a song flight, landing near a Blackcock which flew off after a few seconds. (c) A Red Grouse ran towards a Greyhen feeding on oats outside a wire-netting trap and she immediately flew off (d) A Blackcock flew for 3 m at a Red Grouse which then flew away.

(iii) Attack, four times. - (a) With heads forward and combs raised, two Red Grouse ran towards two Blackcocks and a Greyhen feeding on heather. The Greyhen flew off with one Blackcock; the other Blackcock then walked away, in a submissive posture. (b) A Red Grouse gave a song flight to land 5 m from two Greyhens, which ran away, and he chased them, with raised combs. (c) A Red Grouse approached a Greyhen caught in a trap on oat stubble, scratched at the wire with his feet, walked round the trap following her, and then jumped on top of the trap with combs raised, whilst she fluttered trying to escape. (d) A Red Grouse gave a song flight, landing near a Black cock which flew a few metres, chased by the Red Grouse. They landed and briefly faced each other, but when a second Red Grouse gave a song flight nearby, they broke off and all three started feeding.

(iv) Prolonged encounter for several minutes, three separate occasions - A Red Grouse and Blackcock faced each other 1 m apart and stepped sideways along a line; the Red Grouse bobbed his head with combs raised, showing a posture and calls indicating attack intention (Watson and Jenkins 1964); the Blackcock fanned his tail, drooped his wings, took up a horizontal posture (Johnstone 1969), and hissed. In all three encounters the Blackcock broke off first, and showed a submissive posture while walking away.