

Brief report

Neighbour interference in Lapwing *Vanellus vanellus* nest defence

Gaute Bø Grønstøl & Kjell-Magne Pedersen

Grønstøl, G. B. & Pedersen, K.-M., University of Bergen, Institute of Zoology, Department of Ecology, Allégt. 41, N-5007 Bergen, Norway

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Lapwings are known to nest in semicolonial aggregations, probably due to the benefits of communal defence against nest predators (e.g. Göransson et al. 1974, Elliot 1985ab). Within such a communal defence umbrella of mutual benefits, one might find that birds attempt to exploit existing opportunities to maximize individual success at their neighbours' expense. In two species of polyandrous Jacanas, *Jacana spinosa* and *J. jacana*, females are reported to kill the chicks of other females when males are in deficit, in order to get the males to incubate their own clutches (Stephens 1982, Emlen et al. 1989). Similar behaviour is also reported for three passerine species (Freed 1986, Veiga 1990, Bensch 1993). In studies of the Hooded Crow's *Corvus corone cornix* response to dummy crows and a dummy Eagle Owl *Bubo Bubo*, Slagsvold (1984, 1985) proposed that components of the mobbing behaviour of dominant males (i.e. a tendency to inhibit other males from mobbing a victim) served a role in self-advertisement. In a study of Lapwing responses to a model predator, we found indications that male Lapwings interfered with their neighbours, possibly to increase their own fitness through usurpation of resources from males that suffer nest-predation, or increasing their own attractivity and dominance status relative to other birds.

On a grassland area at Haukås in Bergen, western Norway, we introduced a model predator (a commercially manufactured Herring Gull *Larus argentatus*) into the territories of male Lapwings with incubating females in order to investigate nest

defence behaviour. This is a dense breeding population, and in 1992, when this study was made, 41% of the males bred with 2 or 3 females on their territory simultaneously. We could identify individual birds by plumage differences on the face, breast and coverts (Byrkjedal et al. 1997).

The model was placed 6 m from the nests four times on each of the 17 territories during the incubation and early chick period. In polygynous territories the model was placed between the nests at a distance of 6 m from one of them. The model was left on the territory for five minutes and Lapwing responses were video recorded. Comments on the observed behaviour and identity of the birds were read into the video recorder microphone; the identity of the birds was determined upon landing.

The resident male usually responded with the highest intensity, often hitting the model with his wing. But, the nesting female and nearby nesting males and females also dived at the model. Neighbouring males were on several occasions observed to interfere with the defence of the resident males. The territory owner would typically dive at the model from a height of approximately 5–6 m, upon which a neighbouring male would intercept the defending male and deflect the attack dive, which would force the territory owner to change course some 1.5–3 m from the model. While the trajectory of the resident male's dive was aimed towards the model, the intervener's dive was directed at a point immediately ahead of the defender, usually parallel to the model and approaching the resident male from the side, indicating that the resi-

dent male, and not the model, was the target for the attack. Such interferences were recorded in 24 out of 68 experimental bouts on 12 of 17 territories. One trigamous male was responsible for the interference in 15 of these cases, of the remaining 9 we could attribute two of the interceptions to two monogamous males. The identity of the remaining interveners is unknown. In three of the experimental bouts the resident male was attacked continuously throughout the whole five-minute period. On four occasions, on three different territories, the resident female was attacked while attempting to deter the model predator; two of these females were monogamous and two were paired with a trigamous male.

In 10 of the 24 bouts where interference was registered, the harassed resident male (or in two cases his female) was monogamous, at 4 bouts the attacks were directed against bigamous males, and in 10 bouts the attacks were directed against trigamous males (or in two cases one of his females). In 7 of the bouts the interferer also took some dives at the model. This only occurred at territories immediately adjacent to the interferer.

As some interactions took place outside of the video recorded sector, and given the difficulty of identifying and following several birds in the air at the same time, these results are likely to be conservative estimates of the frequency at which this behaviour occurred.

If the female deserts the male after her nest is attacked, neighbouring males would get a chance to increase their territory at the cost of the resident male. They would also have a chance to gain extrapair-fertilizations with the robbed female, or to attract her to their territory in her prelaying period before a replacement clutch. If the female decides to stay with the same male after predation, the maintenance of his territory (which requires regular engagements in competitive encounters along the territory borders) might be compromised by his need for mate guarding, thus providing an opportunity for neighbours to expand their territory.

Another explanation might be reduction of post-hatching competition over favourable foraging areas for the chicks. After hatching, the chicks are dependent on short vegetation to forage effectively (Galbraith 1988, Beintema 1990). Competitive interactions over such areas were com-

monly seen at Haukås during the first week after hatching in 1992. By indirectly forcing adjacent females to restart breeding, the synchronicity of the hatching time between his own clutch and that of the neighbour is decreased, which would reduce the competition over good foraging areas for the chicks.

The observation that interfering males also dived at the model indicates either that they were torn between the urge of responding to the threat so close to their territory and the drive to sabotage the nest defence, or, as Slagsvold (1984, 1985) suggested, that there is a component of self-advertisement in this kind of behaviour. The Lapwing song-flight display contains several aggressively derived components like chases and dives, and they often lead to, or occur after aerial fights (Dabelsteen 1978). Hence, one could guess that assessment of fighting males might be important for the females in their mate choice.

As one male was responsible for a large percentage of the described defence interference, it is difficult to estimate how general this behaviour is in Lapwing populations. More extensive model experiments in dense breeding populations where the identity of the birds is known, combined with investigations of the females' tendency to change mates after nest loss (perhaps by experimentally removing eggs), male mate guarding behaviour, male dominance hierarchy, and male territorial behaviour during mate guarding, could reveal more about the relevance of this behaviour.

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Sammanfattning: Grannhanar stör Tofsvipors boförsvär

I denna studie undersöktes gruppäckande tofsvipors reaktion på en gråtrutmodell som placerats på deras revir. I 24 av 68 försök, omfattande 12 av de 17 studerade reviren, blev den residenta hanen förhindrad i sina angrepp på modellen av grannhanarna. Leder denna inblanding i boförsvaret till ökade eggföruster gynnas grannhanarna genom att de 1) kan utvida sina revir, 2) ökar sina möjligheter att locka till sig honan eller genom

extraparfertilisering befrukta hennes omlagda ägg, 3) minskar konkurransen om goda näringsplatser för sina ungar pga minskad äggkläckningssynkronitet och/eller 4) ökar sin egen status. Det verkar alltså som om viphanar försöker maximera sin egennyttan på andres bekostnad, till och med under det gemensamma boförsvaret.

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