Ornis Fennica 79:82–86. 2002

Brief report

Defensive behaviour by Jackdaws (*Corvus monedula*) in response to cooperative hunting of Lanner Falcons (*Falco biarmicus*)

Giovanni Leonardi

Leonardi, G., Dipartimento di Biologia Animale dell'Università di Catania, Via Androne, 81, I-95124 Catania, Italy. (Present address: Via Santangelo Fulci, 28, I-95127 Catania, Italy.) E-mail: areleo@yahoo.com

Received 15 February 2000, accepted 17 November 2000

1. Introduction

When a predator attacks prey several factors can affect the likelihood of success (Götmark & Post 1996). Previous studies have shown that prey group size, type of attack and escape response could influence the success of an attack independently (Buitron 1983, Lima & Dill 1990, Pettifor 1990, Cresswell 1993, 1994). The optimal choice of defence of a prey may also depend on the number of predators attacking (Lima 1992, Hori 1993), as prey vigilance is effective mainly for single predator strikes and not for group attacks (Buchanan *et al.* 1988, Dekker 1988, Cresswell 1993, 1994, Lima 1995). Active responses of the prey could decrease the capture ratio (Leonardi 1991, Cresswell 1994, Leonardi 1999). In addition, large groups of prey, due to their conspicuousness, stimulate attacks from predators (Hector 1986, Ellis *et al.* 1993, Krause & Godin 1995, Leonardi 1999). It is likely that a trade-off between risks of injury and response intensity can be expected. In Sicily, Jackdaws (*Corvus monedula*) nest in association with Lanner Falcons (*Falco biarmicus*) despite having a high risk of predation (Massa *et al.* 1991, Leonardi 1999). I studied this population system to determine if defensive responses depended on group sizes, predator number or type of attack.

2. Material and methods

This study was conducted at five sample sites in central eastern Sicily during three reproductive periods of the Lanner Falcon (1988–1990). The main habitat is an agro-ecosystem of orchards and wheat monoculture with small islands of natural areas of shrubs and bushes (Leonardi 1994,1999). Each breeding site was visited 10 times mainly in the early morning, a total of 55 hours. In Sicily the coexistence of specialized predators like Peregrines (*Falco peregrinus*) and Lanner Falcons and its possible prey is common in spite of predation risks (Massa *et al.* 1991, Leonardi 1994). Although in general, prey lives far from potential predators, Jackdaw nesting colonies were found close to the nest-site of the Lanner Falcons (Wiklund 1982, Sodhi *et al.* 1990, Suhonen *et al.* 1994). In Jackdaw colonies, the number of individuals fluctuated from 20 to 70. Generally they occupied 3–5 large ledges in the centre of the rock

cliff (n = 12, unpublished data). The daily pattern of activity and social behaviour of Jackdaws was observed and flock sizes into three size classes according to other studies: 2–10, 11–30 and 31–50 individuals (Kenward 1978, Buitron 1983, Cresswell 1996). As shown in Table 1, mobbing, escape and alarm calls were recognized as different responses towards attacking Lanners (Buitron 1983). In falcon pairs the small male attacked first and the female generally caught the prey. They attempted to avoid prey defensive responses, allocating the hunting efforts (Leonardi 1999). Statistics were analysed using SyStat 9.0 statistical program (SPSS Inc. 1998). Yates' correction was used in chi-squared and Williams' correction in G-tests (Zar 1984).

3. Results and discussion

In general the defensive choice of Jackdaws depends on the flock size ($G_4 = 16.6, P < 0.001, n = 58$, Fig. 1). The large group has exhibited all defensive actions in response to attacks; they consisted mainly of mobbing ($\chi^2_2 = 15.9, P < 0.001, n = 31$, Fig. 1). According to the model of Turner and Pitcher (1986) it is advantageous to be in a larger flock during a predator attack. Field evidence supported this theory as far as the probability of detection and subsequent attack by predators did not increase with increasing group size (Cresswell 1994, Krause & Godin 1995). In fact, during cooperative hunting many individuals were involved in the defensive action producing confusion, but they incurred high per capita risks in terms of number of attacks and attack duration (Turner & Pitcher 1986, Krause & Godin 1995, Leonardi 1999). Presumably, Jackdaw flocks enhanced their survival chances by mobbing as well as by the flock benefits. For the small sized flocks the low conspicuousness limited the encounter rate by predators. Mobbing is less significative in comparison with other defence responses (Fig. 1). It seems that the reaction of the Jackdaw can be stimulated by the presence of single attacking individuals, apart from pairs of Lanners ($G_4 = 14.8$, $P < 0.005$, $n = 58$, Fig. 2). Particularly, large groups of Jackdaws mobbed the female of Lanner Falcon (Fisher exact test $P = 0.032$, $n = 14$) whereas small flocks of Jackdaws generally escaped ($\chi^2_2 = 7.6$, $P < 0.05$). On the contrary, the attacks by male Lanners did not encourage strong responses by the prey; they mainly uttered alarm calls (Fisher exact test $P = 0.024$, $n = 14$, Fig. 2). The risk represented by the female of Lanner is due to its size, which allows capturing large prey like the Jackdaw. The great capture success of the female, during the cooperative hunting, can support this hypothesis (Yosef 1991, Leonardi

Table 1. Characterization of prey and predator behavioural patterns observed in five nesting colonies of Jackdaws during cooperative hunting attempts of the Lanner Falcon.

	Description	References
Prey defense behaviours		
Mobbing	Prey flocks close dive upon predators with an evasive flight	Buitron 1983, Pettifor 1990
Alarm	Perched prey gave alarm call or followed at a distance	Buitron 1983
Escape	Prey flocks fly away from predators	Buitron 1983, Cresswell 1994
Predator attacks		
Surprise attack	Predators first approach close to prey from behind rock cliffs	Cresswell 1994, 1996, Leonardi 1999
Non-surprise attack	Both predators are visible at the onset of attacks, then they try to encircle prey flocks.	Cresswell 1994, 1996, Leonardi 1999.
Partial-surprise attack	One of the two attacking predators is visible to prey while the other one attacks by surprise. Both perched predators would depart at different times.	Cresswell 1994, 1996, Leonardi 1999.

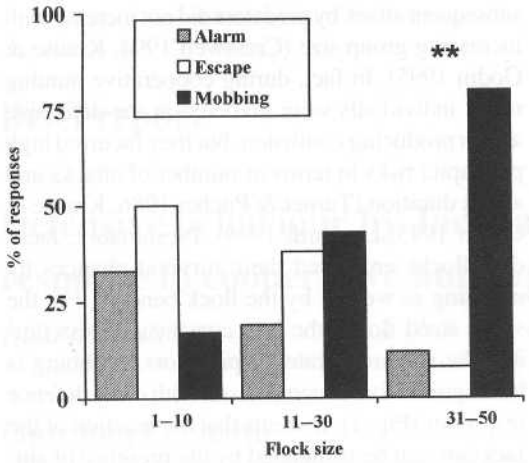

Fig. 1. Defensive action percentages according to flock sizes classes Jackdaws (n = 12 for 1–10; n = 21 for 11–30; n = 25 for 31–50). ** denotes P < 0.001.

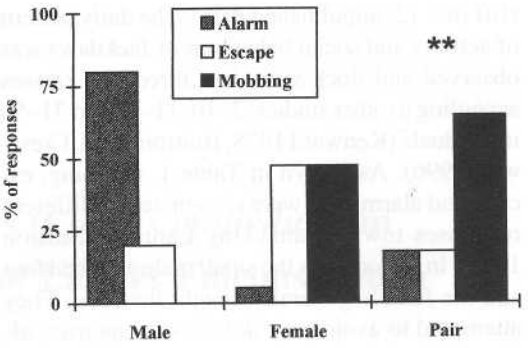

Fig. 2. Defensive techniques of the Jackdaw flocks observed in presence of paired and single Lanners (n = 5 for male; n = 19 for female; n = 34 for pairs). ** denotes P < 0.001.

1999). Thus, the recognition of sexes through the identification of the size, plays a very important role in the choice of the correct counterattack. Nevertheless, the low reaction of the Jackdaws towards the male predators is potentially dangerous during the partial surprise attacks, during the first attack (Leonardi 1999). In response to the different hunting techniques of the Lanner, Jackdaws use single defensive actions or a combination of them (Table 2). The significant result between the mobbing and the non- and partial-surprise attacks shows the important role of the visual detection during the surprise strikes (Table 2, Lima 1995). The escape tactic appaears to be the most effective response to unexpected attacks (Table 2, Leonardi 1991, Cresswell 1993, 1996). Probably, the high proximity to predators, removing other menaces for the prey, has also the advantage of a better visibility during attacks (Wiklund 1979, Paine *et al.* 1990).

Table 2. Defensive actions in responses to Lanner Falcon cooperative attacks (alarm n = 11; escape n = 16; mobbing n = 31). * denotes P < 0.05, ** denotes P < 0.001, and *** denotes P < 0.0001.

	Alarm	Escape	Mobbing
Surprise	5	10	1 *
Non-surprise	5	2	20 ***
Partial surprise	1	4	10 *
	n.s.	*	**

Available data on the diet of the Lanner Falcon in Sicily showed a high frequence of predation of Jackdaws (6% to 36%) (Mebs 1959, Massa *et al.* 1991). The vigilance can reduce the success rate of an open attack, so that Jackdaws remain relatively safe in falcon's areas. This study suggests that Lanners use paired attacks to counter the defensive behaviour of Jackdaws. Therefore, it predicts that the attack success rate of pairs will be higher than of single Lanners. In this context, Jackdaws may compensate for the increased predation risk presented by grouped predators by adopting defensive mobbing behaviour. This evidence shows that jackdaws distinguish between the predation risks of different contexts. In addition, jackdaws respond appropriately to different predation risks.

Acknowledgements: I gratefully thank Alan Kemp, C. M. White, R. Yosef and two anonymous reviewers for their helpful comments and suggestions on an earlier draft. I greatly appreciate the improvements made in English usage by Gudrun Hilgerloh and Daniel English.

Selostus: **Naakan puolustuskäyttäytyminen välimerenhaukan yhteissaalistuksen vastineena**

Useat tekijät voivat vaikuttaa hyökkäyksen tuloksellisuuteen, kun peto hyökkää saalistaan kohti. Tutkimukset ovat osoittaneet, että saaliin ryhmäkoko, saaliin käyttäytyminen ja pedon hyökkäystyyli vaikuttavat hyökkäyksen onnistumiseen toisistaan riippumatta. Saaliin optimaalinen puolustuskäyttäytyminen on riippuvainen myös hyökkäävien petojen määrästä, koska saaliin tarkkaavaisuus on tehokkaimmillaan yksittäisen pedon hyökätessä. Artikkelin kirjoittaja tutki Italiassa vuosina 1988–1990, kuinka naakat käyttäytyivät välimerenhaukkojen hyökätessä niiden pesäkoloniaan. Naakka on Italiassa tärkeä välimerenhaukan saalislaji. Pesivien naakkojen määrä kolonioissa oli 20–70 yksilöä viidellä tutkimuksessa mukana olleella alueella. Pedon hyökätessä koloniaan naakat joko pakenivat tai alkoivat varoitella tai ahdistella petoa. Kun naakkayhdyskunta joutui välimerenhaukkaparin hyökkäyksen kohteeksi, naakat yleensä alkoivat ahdistella haukkoja. Naakkojen puolustuskäyttäytyminen oli riippuvainen naakkojen määrästä. Mikäli naakkoja oli koloniassa paljon (vähintään 31 yksilöä), naakat reagoivat petoon yleensä ahdistelemalla petoa. Jos naakkoja oli koloniassa vähemmän, petojen ahdistelu oli vähäisempää verrattuna muihin saaliin reagointitapoihin. Mikäli haukka pääsi yllättämään kolonian, naakat yleensä pakenivat. Jos hyökkääjänä oli koirashaukka yksin, naakat useimmiten vain varoittelivat. Koirashaukan ja naarashaukan yhteissaalistuksessa isokokoisen naarashaukan menestys saalistajana oli hyvä. Tutkijan mukaan kooltaan isompi välimerenhaukkanaaras on suurempi uhka naakoille kuin pienikokoisempi koiras. Välimerenhaukkanaaras kykenee erityisen menestyksellisesti saalistamaan myös suurikokoisia kohteita, kuten naakkoja. Tutkija päätteleekin, että naakat voivat saalistajan koosta arvioida, kuinka suuri uhka lähestyvä peto kolonialle on ja millä tavalla saalistajaan tulee reagoida. Kirjoittajan mukaan haukkojen kannattaisi hyökätä naakkakoloniaan pareittain. Vastaavasti naakkojen kannattaisi puolustautua pareittain hyökkääviä välimerenhaukkoja kohtaan käymällä vastahyökkäykseen. Hyvä näkyvyys voi heikentää haukkojen saalistuksen onnistumistodennäköisyyttä avoimilla alueilla. Tämä voi mahdollistaa naakkojen ja välimerenhaukkojen rinnakkaiselon alueella. Tulokset osoittivat, että naakat reagoivat petoon eri tavoin eri tilanteissa.

References

Buchanan, J. B., Schick, C. T., Brennan, L. A. & Herman, S. G. 1988: Merlin predation on wintering Dunlins: hunting success and Dunlin escape tactics. — Wilson Bull. 100: 108–118.

Buitron, D. 1983: Variability in the responses of black-billed magpies to natural predators. — Behaviour 87: 209–236.

Cresswell, W. 1993: Escape by redshanks, Tringa totanus, on attack by avian predators. — Anim. Behav. 46: 609–611.

Cresswell, W. 1994: Flocking is an effective anti-predator strategy in redshanks, Tringa totanus. — Anim. Behav. 47: 433–442.

Cresswell, W. 1996: Surprise as a winter hunting strategies in Sparrowhawks Accipiter nisus, Peregrines, Falco peregrinus, and Merlins, F. colombarius. — Ibis 138: 684–692.

Dekker, D. 1988: Peregrine Falcon and Merlin predation on small shorebirds and passerines in Alberta. — Can. J. Zool. 66: 925–928.

Ellis, D. H., Bednarz, J. C., Smith, D. G. & Flemming, S. P. 1993: Social foraging classes in raptorial birds. — BioScience 43: 14–20.

Götmark, F. & Post, P. 1996: Prey selection by sparrowhawks, Accipiter nisus: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. — Phi. Trans. R. Soc. Lond. B 351: 1559–1577.

Hector, D. P. 1986: Cooperative hunting and its relationship to foraging success and prey size in an avian predator. — Ethology 73: 247–257.

Hori, M. 1993: Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. — Science 260: 216–219.

Kenward, R. E. 1978: Hawks and Doves: factors affecting success and selection in Goshawk attacks on

Woodpigeons. — J. Anim. Ecol. 47: 449–460.
Krause, J. & Godin, J.-G. J. 1995: Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. — Anim. Behav. 50:465–473.
Leonardi, G. 1991: Osservazioni preliminari sull'eco-etologia del Lanario Falco biarmicus feldeggi in Sicilia. — Suppl. Ric. Biol. Selvaggina 17: 147–149.
Leonardi, G. 1994: The home range of the Lanner Falco biarmicus: influences of territory composition. — In Meyburg, B.-U. & Chancellor, R. D. (eds.), Raptor Conservation Today: 153–155. WWGBP & Pica Press, Berlin, Germany.
Leonardi, G. 1999: Cooperative hunting of Jackdaws by the Lanner Falcon (Falco biarmicus). — J. Raptor Res. 33: 123–127.
Lima, S. L. 1992: Life in a multi-predator environment: some considerations for anti-predator vigilance. — Ann. Zool. Fenn. 29: 217–226.
Lima, S. L. 1995: Back to the basics of anti-predatory vigilance: the group size effect. — Anim. Behav. 49: 11–20.
Lima, S. L. & Dill, L. M. 1990: Behavioural decisions made under the risk of predation: a review and prospectus. — Can. J. Zool. 68: 619–640.
Massa, B., Lo Valvo, F., Siracusa, M. & Ciaccio, A. 1991: Il Lanario (Falco biarmicus feldeggi Schlegel) in Italia: status, biologia e tassonomia. — Il Naturalista Siciliano 15: 27–63.
Mebs, T. 1959: Beitrag zur Biologie des Feldeggsfalken (Falco biarmicus feldeggi). — Vogelwelt 80:142–149.
Paine, R. T., Wootton, J. T. & Boersma, P. D. 1990: Direct and indirect effects of Peregrine Falcon predation on seabird abundance. — Auk 107:1–9.
Pettifor, R. A. 1990: The effects of avian mobbing on a potential predator, the European kestrel, Falco tinnunculus. — Anim. Behav. 39: 821–827.
Sodhi, N. S., Didiuk, A. & Oliphant, L. W. 1990: Differences in bird abundance in relation to proximity of merlin nests. — Can. J. Zool. 68: 852–854.
SPSS Inc. 1998: SyStat 9.0 — Chicago, Illinois, U.S.A.
Suhonen, J., Norrdahl, K. & Korpimäki, E. 1994: Avian predation risk modifies breeding bird community on a farmland area. — Ecology 75: 1626–1634.
Turner, G. F. & Pitcher, T. J. 1986: Attack abatement: a model for group protection by combined avoidance and dilution. — Am. Nat. 128: 228–240.
Wiklund, C. G. 1979. Increased breeding success for Merlins Falco colombarius nesting among colonies of Fieldfares Turdus pilaris. — Ibis 121: 109–111.
Wiklund, C. G. 1982: Fieldfare (Turdus pilaris) breeding success in relation to colony size,nest position and association with Merlins (Falco colombarius). — Behav. Ecol. Sociobiol. 11:165–172.
Yosef, R. 1991: Foraging habits, hunting and breeding success of Lanner Falcon (Falco biarmicus) in Israel. — J. Raptor Res. 25:77–81.
Zar, J. H. 1984: Biostatistical analysis. — Prentice-Hall Inc., Englewood Cliffs, NJ U.S.A.