BROWN BOOBY *SULA LEUCOGASTER* GROUP SIZE AS A DEFENSE AGAINST KLEPTOPARASITISM

DAVID C. DUFFY

Pacific Cooperative Studies Unit, Department of Botany, University of Hawaii Manoa, 3190 Maile Way, Honolulu, Hawai'i 96822, USA (dduffy@hawaii.edu)

Received 16 December 2014, accepted 2 February 2015

Kleptoparasitism, or food piracy, is widespread among seabirds (Brockmann & Barnard 1979, Furness 1987), leading seabirds to adopt various strategies to avoid being parasitized. These include choice of nesting location (Nettleship 1972), changes in flight altitude and behavior when approaching the colony or nest site (Grant 1971), diving underwater to escape aerial pursuit (Grant 1971), avoiding situations in which the ratio of parasites is large relative to potential victims (Grant 1971, Blackburn *et al.* 2009) and decreasing the same ratio by defensively aggregating as flocks, as do other organisms (e.g. Hamilton 1971, Falconer 1976, Courchamp *et al.* 2002, Carbone *et al.* 2005). This note reports on the apparent use of the last strategy by Brown Boobies *Sula leucogaster* to avoid parasitism by Magnificent Frigatebirds *Fregata magnificens*.

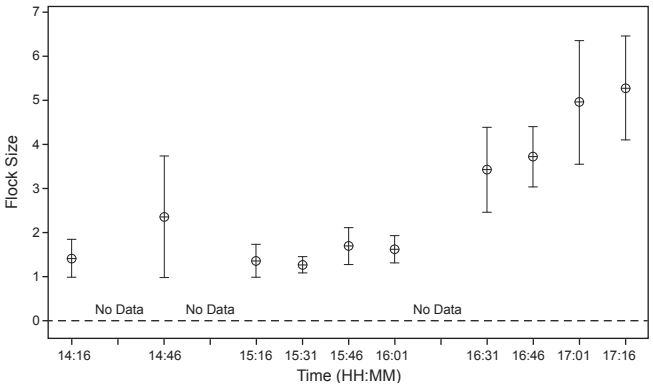

Fig. 1. Flock size of Brown Boobies (number of birds) returning to Isla Santa Catalina, Ecuador, over time on 21 November 1993 (central point is mean and error bars are 1 standard error).

We (myself and Luke Hoch, see Acknowledgements) observed Brown Boobies returning from the open ocean to the nesting colony on Isla Santa Catalina, Ecuador (10°51′15.85″N, 85°55′51.92″W), during two afternoons, 19 and 21 November 1993. We made our observations from a 6 m open boat located approximately 0.5 km west of the island. On 19 September we observed from 16h20 to 17h30, and on 21 September from 14h15 to 17h30. Sunset was at approximately 16h40. Winds were <10 km/h, waves were <1.0 m, and the sky was clear. We counted the number of individuals and flocks of boobies returning to the island, the size of booby flocks, and the number of frigatebird kleptoparasitic attacks. Perhaps 30 frigatebirds were in the area, but as they were dispersed widely and then converged for attacks, an accurate number was difficult to obtain. We did not record the number of frigatebirds per attack, because birds joined or left during an attack, or approached but did not participate. Total or mean number of piratic frigatebirds might have affected both probability of attack and outcome, but we had no way of recording such dynamic events. We also could not record success rates because some attacks ended over or behind the island.

For analysis, we combined the data from the two days to examine group size, frequency of kleptoparasitic attempts per group and the probability per bird of attacks in groups of different sizes. To examine group size over time, we used only the data from 21 November, as it represented the longest time span.

Boobies returned to the island at heights ranging from 3 to 50 m. Frigates circled anywhere from over the island to at least 0.5 km from the island at elevations usually higher than the greatest elevation of the island (50 m). Attacks occurred at sea, but some continued to the island.

TABLE 1
Probability of Magnificient Frigatebird attacks on Brown Boobies by flock size and number

Flock size	No. observations	No. birds	No. attacks	Probability attack/flock	Probability attack/bird
1	110	110	34	30.9	30.9
2 to 5	60	183	5	9.5	2.7
6 to 10	27	192	7	25.9	3.5
11 to 20	18	278	10	55.5	3.6
20+	13	369	7	53.8	1.7
Total	67			35.12	

We recorded 228 sightings of returning boobies as singletons or as flocks, totaling 1 132 individuals, and noted 63 attacks by frigatebirds. There was a 27.6% probability of attack on a flock across all sizes, but attack probability ranged from 11.8%/bird for flocks of two to five, to 53.8%/bird for flocks >20 (Table 1). Excluding single birds, probability of attack per flock varied significantly with flock size ($\chi^2 = 14.3$, $P = 0.0038$). However, when the probability per bird was calculated, the situation was reversed. Single birds had an attack probability of 30.9% while individuals in flocks >20 had only a 1.9% chance of being attacked (Fisher's exact test, $P < 0.05$). On 19 September, our longest span of observation, group size increased significantly over time ($r_s = 0.806$, $P = 0.005$; Fig. 1).

Results indicated that increasing flock size in Brown Boobies led to increased probability of attack by Magnificent Frigatebirds on the group, but decreased risk per bird, as predicted by Hamilton's selfish herd hypothesis (1971). Boobies approaching the nesting island over open ocean would have no way to hide from frigatebirds unless they returned at night. LeCorre & Jouventin (1997) reported a similar relationship of increased attacks but decreased risk per individual for larger groups of Red-footed Boobies *Sula sula* by Great Frigatebirds *F. minor* at Europa Island, Indian Ocean. In contrast, Vickery & Brooke (1994) found that, while single Masked Boobies *Sula dactylatra* were more likely to be attacked than were groups at Henderson Island, South Pacific, the relationship disappeared when height of the booby flock was taken into account. Since we observed from sea level, we had no accurate way to determine height.

In the present situation, flock size increased progressively later in the day, so that probability of attack per bird grew smaller, suggesting that later birds had more chance of successfully delivering food to their young. However, birds that were more efficient at foraging would presumably return earlier to feed their young, but this would also expose them to greater chance of kleptoparasitic attack, as they would be alone or part of smaller returning flocks. However, more efficient foragers might also be more efficient at avoiding attackers or might have time to return to the feeding grounds to acquire a replacement meal following a successful piracy.

ACKNOWLEDGEMENTS

I thank Luke Hoch of the *Caroline* for his enthusiastic help in making these observations possible, Daniela Dutra Elliott for helping with data analysis and Stephanie Joe for crafting the figure. I am very grateful for assistance from the National Geographic Society through Grant 4392-90: Seabirds of the Gulf of Papagayo.

REFERENCES

BROCKMANN, H.J. & BARNARD, C.J. 1979. Kleptoparasitism in birds. *Animal Behaviour* 27: 487–514.

CARBONE, C., FRAME, L., FRAME, G., MALCOLM, J., FANSHAWE, J., FITZGIBBON, C., SCHALLER, G., GORDON, I.J., ROWCLIFFE, J.M. & DU TOIT, J.T. 2005. Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. *Journal of Zoology* 266: 153–161.

COURCHAMP, F., RASMUSSEN, G.S.A. & MacDONALD, D.W. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioural Ecology* 13: 20–27.

FALCONER, N. 1976. On the size of convoys: an example of the methodology of leading wartime OR scientists. *Operational Research Quarterly* 27: 315–327.

FURNESS, R.W. 1987. Kleptoparasitism in seabirds. In*:* Croxall, J.P. (Ed.) Seabirds: feeding ecology and role in marine ecosystems. Cambridge, UK: Cambridge University Press. pp. 77–100.

GRANT, P.R. 1971. Interactive behaviour of puffins (*Fratercula arctica L.*) and skuas (*Stercorarius parasiticus L.*). *Behaviour* 40: 262–281.

HAMILTON, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295–311.

LeCORRE, M. & JOUVENTIN, P. 1997. Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the Red-footed Booby. *Condor* 99: 162–168.

NETTLESHIP, D.N. 1972. Breeding success of the Common Puffin, (*Fratercula arctica*) on different habitats at Great Island, Newfoundland. *Ecological Monographs* 42: 239–268.

VICKERY, J.A. & BROOKE, M.D.L. 1994. The kleptoparasitic interactions between Great Frigatebirds and Masked Boobies on Henderson Island, South Pacific. *Condor* 96: 331–340.