

APOSTATIC SELECTION AND KLEPTOPARASITISM IN THE PARASITIC JAEGER: A COMMENT

BRIDGET L. FURNESS¹ AND ROBERT W. FURNESS²

¹*Cullerty Field Station, University of Aberdeen, Newburgh, Ellon, Aberdeenshire AB4 0AA, Scotland* and ²*Zoology Department, Glasgow University, Glasgow G12 8QQ, Scotland*

ABSTRACT.—There are conflicting ideas on the factors that affect color-phase polymorphism in Parasitic Jaegers (*Stercorarius parasiticus*). O'Donald and Davis (1975) believe that the polymorphism is transient. Arnason (1978) believes that the polymorphism is balanced and maintained by apostatic selection, in which the rare form is at a selective advantage because its prey do not have a chance to form a "search image" of it. At one colony in Iceland he found that the pale birds were significantly more successful than the dark. Data we collected at Iceland and Shetland show no significant difference in success between the two phases. We conclude that it is unlikely that apostatic selection maintains a balanced polymorphism. We feel it is more likely that a combination of sexual selection and assortative mating (O'Donald and Davis 1975) are the major factors affecting this polymorphism. *Received 11 March 1980, accepted 5 July 1980.*

THE Parasitic Jaeger (*Stercorarius parasiticus*) exists in dark, intermediate, and pale phases. These color phases are determined by two alleles at a single locus (O'Donald and Davis 1959). The head, neck, and underparts of the dark phase are a sooty brown color. The intermediate has whitish-buff sides of the head and sometimes paler brown underparts. The pale phase is strikingly different from the two dark forms. Its underparts are completely pale, and the pale coloring extends to the nape and cheeks. There is sometimes a buff band across the breast. In this study the dark and intermediate birds have been treated as one group because they are so similar in appearance. True dark and pale birds are homozygotes, while most intermediates are heterozygotes, but, because dark and intermediate birds are so similar, a small number of individuals that are classified as dark are heterozygotes.

The geographic data (Southern 1943) show a cline in frequency of the dark allele, suggesting that the light phase has a selective advantage in the north and that dark birds have a selective advantage in the south of the breeding range. O'Donald and Davis (1975), however, believe that the polymorphism is transient. They have shown that dark males are favored through sexual selection because in new pairs they start breeding earlier in the season than other new males. This gives them a selective advantage because early pairs fledge more chicks than pairs breeding later. Pale birds of both sexes have a selective advantage because they start to breed at an earlier age than do other phases and on average will raise more young in their reproductive life. The component of selection in favor of pale birds is greater than that in favor of dark males. Using computer modelling, O'Donald and Davis (1975) have predicted that the pale phase will replace the other phases over a long period of time.

Arnason (1978), on the other hand, believes that the polymorphism is balanced and maintained by apostatic selection. In this situation the rare form has a selective advantage by virtue of its rarity (Clark 1962a, b, 1969). Arnason (1978) has suggested that the rare phase, in his case the pale morph, should be a more successful kleptoparasite because the prey will have less chance to form a "search image" of that phase because of the decreased frequency of encounter.

TABLE 1. The percentage of successful chases made by dark and pale Parasitic Jaegers of different species at each colony studied.

Colony	Year	Species chased	Per-centage of dark successful	Number of chases	Per-centage of pale success-ful	Number of chases	χ^2 exact prob-ability	Fisher's exact prob-ability
Iceland								
Höfn	1978	Arctic Tern	23.4	37	15.3	13	—	0.26
Shetland								
Noss	1978	Guillemot	12.6	119	22.2	27	0.20	—
Fetlar	1978	Puffin	26.1	46	6.3	16	—	0.09
Foula	1978	Guillemot	0.0	14	16.7	12	—	0.20
Foula	1978	Puffin	25.0	88	15.4	52	0.18	—
Foula	1979	Guillemot	20.7	29	33.3	6	—	0.42
Foula	1979	Puffin	28.2	163	20.3	123	0.12	—
Foula	1979	Arctic Tern	23.4	218	19.0	79	0.42	—

METHODS

In 1978 we visited Iceland and Shetland to study the kleptoparasitic behavior of Parasitic Jaegers. Observations were made close to large breeding colonies (>30 pairs, Höfn, Iceland; 270–300 pairs, Foula; 35–40 pairs, Noss; 200–220 pairs, Fetlar, Shetland) in order to avoid biases that could be caused by differences between individuals irrespective of phase. In 1979 a detailed study was carried out on Foula, Shetland, where 300 pairs were breeding in an area of only 1.7 km². In Shetland and Iceland the pale phase is much less common than the dark, there being 27% in south Iceland and 23–24% in all Shetland colonies (Berry and Davis 1970). For periods of 1–2 h on alternate days through the breeding season BLF watched jaegers searching for and chasing seabirds. The phase of the individual chasing, the species that were chased, and chase success (success = victim dropped fish) were recorded. The speed of the victim's reaction was also recorded by scoring it in one of three categories (Furness 1978): (1) the victim began evasive action (accelerated flight or dive towards the sea) as soon as the jaeger had begun directed flight; (2) the victim's speed of reaction was intermediate between 1 and 3; and (3) the victim did not begin evasive action until the jaeger had almost reached it. Using these methods, factors other than color phase that influence chase success were examined by Furness (1978).

RESULTS

At Höfn, Iceland only Arctic Terns (*Sterna paradisaea*) were seen to be chased. Guillemots (*Uria aalge*) were the main victim at Noss, Shetland, while puffins (*Fratercula arctica*) were the main species chased at Fetlar. At Foula, puffins were the main victim in 1978, while in 1979 large numbers of Arctic Terns were also chased. There were no differences in the success of chases by pale and dark phase Parasitic Jaegers of different species, although chase strategies and success rates do vary between species (Table 1; Furness 1978, Furness in press). None of our results supports Arnason's prediction that, where they are the rare form, the pale phase should be more successful.

Andersson (1976) has suggested that the dark phase is more common in Shetland and other southerly breeding grounds because it is using "aggressive camouflage." He suggests that this phase is less conspicuous against sea and cliffs and so should be more successful. He presented no data to support this idea. We also feel that dark phase birds are more difficult to locate against a dark background. Our data do not suggest, however, that aggressive camouflage is used by the jaegers. In no case were dark phase birds significantly more successful (Table 1). Furness (1978)

showed that victim's speed of reaction was an important determinant of chase success. If either Andersson's suggestion or Arnason's hypothesis were correct, we would expect the victim's speed of reaction to be slower in response to the dark phase (aggressive camouflage) or in response to the pale phase (apostatic selection). There was no difference, however, in the victim's speed of reaction to the two phases in 1978 ($n = 424$, $\chi^2_2 = 0.26$, $P > 0.1$) or in 1979 ($n = 608$, $\chi^2_2 = 0.45$, $P > 0.1$).

DISCUSSION

In putting forward his hypothesis, Arnason states that the victim will have difficulty forming a "search image" of the rarer phase. We observed that most chases are initiated from above and behind victims as they approach the breeding cliffs. This would result in the jaeger first being seen against the sky. Tinbergen (1951) states that, if a "search image" is formed at all, it is usually of the silhouette of the predator. This would be identical in all phases of Parasitic Jaegers. Further evidence supporting the idea that a "search image" formed is a generalized one, and not of a particular phase or species, comes from situations where Parasitic Jaegers and Great Skuas (*Catharacta skua*) are hunting in the same area. In this situation the presence of one species can decrease the chase success of the other (Furness 1978).

Paulson (1973) has stated that apostatic selection is most effective where predators are hunting a population containing a large proportion of young and naive individuals. Species chased by Parasitic Jaegers in this study are long-lived breeding seabirds that return to the same colony each year, so they should have considerable previous experience of jaegers. The prey species' method of learning is important when considering apostatic selection acting on predators. Available evidence is conflicting. Royama (1970) believes that the "search image" concept has been too uncritically accepted and used as a basis for additional hypotheses (as in Clarke 1962a). For example, there is evidence that reactions of birds to unfamiliar stimuli result in strong "fear and escape" responses (Schleidt 1961). This would make the rare phase of jaeger less successful if victims were to react in this way. There is no evidence to suggest that in this situation they do.

The fact remains that Arnason found a significant difference in hunting success between the two phases. In his study few pale phase individuals were present, so it is likely that the same bird was recorded several times. If there are individual variations in hunting success, as may be expected [see for example Coulson (1972) for a discussion of variations in the quality of individual breeding kittiwakes, *Rissa tridactyla*], this could lead to biased results. This problem may be equally inherent in our own work. At Foula, in 29 watches made in 1979, however, BLF recorded chases by an average of 3.8 pale birds and 8 dark birds each watch. She recorded an average of 21.3 chases per watch, which meant that on average 1.8 chases were recorded per bird. We also noticed that jaegers tend to hunt close to their nesting territories. If observations are made at a fixed point on the coast, mainly locally nesting jaegers will be seen hunting. A few individuals would then provide the bulk of the records. Individual variation in success rate could then lead to a spurious statistical significance, as the observations comprising the data would not necessarily be independent.

If Arnason's data are examined it is evident that the percentage of pale phase birds seen chasing was 5.3% ($n = \text{ca. } 1,680$ observations), while the percentage of pale birds in his study area was 25%. Apparently fewer pale birds were observed

chasing than were present at the colony. From a sample of 226 patrolling birds, Arnason found 12% pale individuals. The ratios obtained from patrolling and chasing birds, however, were calculated from repeated observations of the same individuals, so the lack of independence inherent in these data may account for these discrepancies. BLF found that breeding female Parasitic Jaegers do not leave the territory to feed as often as the males (Furness 1980), which could also account for this discrepancy if the "missing" pale birds were females (i.e. the sex ratios of the morphs were different due to chance).

Furthermore, there would seem to be considerable disagreement as to the ratio of pale to dark birds in the Parasitic Jaeger populations of south Iceland. Bengston and Owen (1973) recorded 11% pale, which is significantly different from the 38% recorded by Southern (1943) ($\chi^2_1 = 33.4$, $P < 0.001$). Berry and Davis (1970) recorded 27% pale phase, which also differs significantly from the ratio of Bengston and Owen ($\chi^2_1 = 21.9$, $P < 0.001$), as does the 25% recorded by Arnason (1978) ($\chi^2_1 = 8.2$, $P < 0.005$). It would seem that the morph ratios may vary between nearby localities, possibly resulting from philopatric tendencies of the young jaegers coupled with local selection pressures or genetic drift (Berry 1977).

It is possible that a balance exists in Britain and Iceland between the theoretical advantages conferred by apostatic selection favoring the pale birds and aggressive camouflage favoring the dark. A test of this would be to examine hunting success of the dark birds in an area where they are the rare phase. They should theoretically have the advantage of rarity and aggressive camouflage, so that victims would react more slowly to dark jaegers, which would have a higher success rate than pale phase birds. This critical test has not yet been made.

In view of the conflicting nature of the data available on this subject, however, we think there is little evidence to support a theory invoking apostatic selection as a force maintaining color-phase polymorphism in the Parasitic Jaeger. Although it is reasonable to expect that high chase success will increase Parasitic Jaeger breeding success, there is as yet little information linking hunting success to output of young in this species, which would be necessary to estimate the selective advantage of successful hunting. We would be inclined to favor the views of O'Donald and Davis (1975) that sexual selection and assortative mating are major factors affecting this polymorphism. The presence of a color polymorphism in the jaegers has still to be explained.

ACKNOWLEDGMENTS

We thank the Holbourn family for allowing us to work on Foula. BLF was supported by a research studentship from the Natural Environment Research Council and thanks Professor G. M. Dunnet for advice and supervision. We are grateful to Drs. P. Monaghan, E. Arnason, W. Hoffman, and M. Andersson for criticism of the manuscript.

LITERATURE CITED

- ANDERSSON, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. *Ibis* 118: 208-217.
- ARNASON, E. 1978. Apostatic selection and kleptoparasitism in the Parasitic Jaeger. *Auk* 95: 377-381.
- BENGSTON, S.-A., & D. F. OWEN. 1973. Polymorphism in the Arctic Skua *Stercorarius parasiticus* in Iceland. *Ibis* 115: 87-92.
- BERRY, R. J. 1977. Inheritance and natural history. *New Naturalist*. London, Collins.
- , & P. E. DAVIS. 1970. Polymorphism and behaviour in the Arctic Skua (*Stercorarius parasiticus* (L.)). *Proc. Royal Soc. London B*(1040): 255-267.

- CLARKE, B. 1962a. Balanced polymorphism and diversity of sympatric species. Pp. 47-70 in *Taxonomy and geography* (D. Nichols, Ed.). Oxford, England, Systematics Association.
- . 1962b. Natural selection in mixed populations of two polymorphic snails. *Heredity* 17: 319-345.
- . 1969. The evidence for apostatic selection. *Heredity* 24: 347-352.
- COULSON, J. C. 1972. The significance of the pair bond in the Kittiwake. *Proc. 15th Intern. Ornithol. Congr.* 424-433.
- FURNESS, B. L. 1980. Territoriality and feeding behaviour of the Arctic Skua *Stercorarius parasiticus*. Unpublished Ph.D. dissertation, Aberdeenshire, Scotland, Univ. Aberdeen.
- . In press. Feeding strategies of the Arctic Skua (*Stercorarius parasiticus*) at Foula, Shetland, Scotland. In *Proc. Symp. on Birds of the Sea and Shore* (J. Cooper, Ed.). Cape Town, Southern African Seabird Group.
- FURNESS, R. W. 1978. Kleptoparasitism by Great Skuas (*Catharacta skua*, Brünn) and arctic skuas (*Stercorarius parasiticus*, L.) at a Shetland seabird colony. *Anim. Behav.* 26: 1167-1177.
- O'DONALD, P., & P. E. DAVIS. 1959. The genetics of colour phases of the Arctic Skua. *Heredity* 13: 481-486.
- , & J. W. F. DAVIS. 1975. Demography and selection in a population of Arctic Skuas. *Heredity* 35: 75-83.
- PAULSON, D. R. 1973. Predator polymorphism and apostatic selection. *Evolution* 27: 269-277.
- ROYAMA, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit (*Parus major* L.). *J. Anim. Ecol.* 39: 619-668.
- SCHLEIDT, W. 1961. Reaktionen von Truthuhern auf fliegende Raubvogel und Versuche zur Analyse ihrer AAM's. *Z. Tierpsychol.* 18: 534-560.
- SOUTHERN, H. N. 1943. The two phases of *Stercorarius parasiticus* (Linnaeus). *Ibis* 85: 443-485.
- TINBERGEN, N. 1951. *The study of instinct*. London, Oxford University Press.