# APOSTATIC SELECTION AND KLEPTOPARASITISM IN THE PARASITIC JAEGER

EINAR ARNASON

*Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA*

ABSTRACT.—The economics of predator avoidance suggest that a prey can act as an apostatic selective agent on its polymorphic predator if it tends to learn an "evil image" of its most common predator more readily than of its rarer predator. Therefore the rare predator morph is expected to catch more prey and it thereby gains a relative advantage over the more common predator morph. Learning among prey that get eaten and the exclusive use of a prey population by one individual predator (territoriality) are problems which are alleviated in the case of the polymorphic klepto-Parasitic Jaegers that hunt on communal grounds. Thus in a locality in southern Iceland where the jaegers rob fish from Common Puffins, light-phased jaegers (the rare morph) were successful in 81% of their attempts whereas the dark-phased ones had a 63% success rate. These observations (based on 3–12 light-phased individuals) accord with the predictions from the apostatic selection hypothesis. To fully test the hypothesis data on the avoidance responses of hosts and the success rate of the two morphs of jaegers are needed from different populations of the Parasitic Jaeger's clinal polymorphism. *Received 15 November 1976, accepted 3 July 1977.*

IN apostatic polymorphism the morphs that stand out from the norm by virtue of their rarity have a selective advantage (Clarke 1962a, 1962b, 1969). This kind of frequency-dependent selection is believed to result from the action of predators which, when maximizing their feeding efficiency, form a "search image" of the most common morph more readily than of the rare morph (Allen 1976, Allen and Clarke 1968, Tinbergen 1960, and see Dawkins 1971). With the predator tending to overlook it just because it is rare, the rare morph gains a relative advantage over the more common morph.

It is reasonable to expect anti-predator behavior to be of selective advantage to prey (Kruuk 1964). The economics of predator avoidance suggest that a prey can maximize its protective advantage if it tends to form an "evil image" of its most common predator more readily than of its rarer predator (Arnason 1974). In this way a prey can act as an apostatic selective agent on its polymorphic predator (Paulson 1973) by responding differentially to the predator morphs. The rare morph will be less familiar to the prey and will thus have a greater hunting success (Paulson 1973).

Recognition of the predator morphs may be learned rather than fixed, which provides for flexibility to deal with changing situations. However, learning presents a problem because prey get eaten. Furthermore, if the predator is territorial, a prey individual may encounter only one of the predator morphs. There are thus two major obstacles to applying the hypothesis of apostatic polymorphism to predators.

The Parasitic Jaeger (*Stercorarius parasiticus*) appears to be an excellent species for testing the hypothesis of apostatic predator polymorphism. Although intermediates exist there are basically two morphs: light- and dark-bellied (Southern 1943). The polymorphism varies clinally with the light morph predominating in the north and the dark morph most common in the south (Southern 1943, Berry and Davis 1970) although some irregularities have been noted (Hildén 1971). O'Donald and Davis (1975 and references therein) suggest that several selective forces are involved (a minor part of which is frequency-dependent sexual selection). They conclude that the polymorphism of the jaeger is transient and that the light morph will eventually

TABLE 1. Success of dark- and light-phased jaegers in inducing puffins to drop their fish

| Number of jaegers | Color of participants in a chase | Number successful | Percent successful | Total number of chases |
|---|---|---|---|---|
| 1 | Dark | 441 | 62.6 | 704 |
| 1 | Light | 25 | 80.7 | 31 |
| 2 | Dark-Dark | 194 | 78.5 | 247 |
| 2 | Light-Dark | 29 | 90.6 | 32 |
| 3 | Dark-Dark-Dark | 56 | 76.7 | 73 |
| 3 | Light-Dark-Dark | 12[a] | 80.0 | 15 |
| 4,5,6 | Dark-Dark-Dark-Dark,-Dark,-Dark | 14 | 73.7 | 19 |
| 4,5,6 | Light-Dark-Dark-Dark,-Dark,-Dark | 8 | 88.9 | 9 |

[a] This category includes a Light-Light-Dark chase, the only instance observed with more than one light-phased individual

replace the dark one. Here I propose that the polymorphism is balanced, being maintained at least partly by apostatic selection.

During a study on jaegers kleptoparasitizing Common Puffins (*Fratercula arctica*) on the south coast of Iceland (Arnason 1974, Arnason and Grant 1977, see also Grant 1971, Grant and Nettleship 1971), I noted the hunting success of the two morphs of jaegers. From late June to early September 1973 I periodically spent a whole day at the puffin cliff studying the behavior of the interactants. The puffins carried fish in the bill to feed their young in the terrestrial burrows at the cliff about 1,000 m from sea where they fed. The jaegers nested in a loose aggregation on the moorland above the cliff. There they held small territories within which they mated, nested, and fed to some extent on arthropods. However, they obtained major parts of their food by kleptoparasitism (Arnason and Grant 1977). The jaegers gathered in the airspace in front of the puffin cliff and patrolled among the incoming puffins. Upon locating a fish-carrier the jaegers chased the puffin and tried to force it to drop the fish. The puffin tried to avoid the jaegers. It often gained speed by descending and headed for safety at the cliff or else it turned back to sea. The jaegers were non-territorial at the cliff; presumably puffins flying at high speed and clumped in space and time (Grant 1971) were a non-defendable resource (Brown 1964).

The light phase was the rarer morph in my study area (9.7% on the south coast of Iceland, Bengtson and Owen 1973). During chases involving a single jaeger the light-phased ones induced puffins to drop their fish in 81% of the chases whereas the dark-phased ones did so in 63% of the chases (Table 1). This difference is significant ($t = 2.21$, $P = 0.014$, one-tailed test of equality of percentages, Sokal and Rohlf 1969: 608). After a jaeger had 'surprised' a puffin and initiated a chase it was frequently joined by other jaegers. A pair of a light and a dark jaeger was significantly more successful in inducing puffins to drop the fish than was a pair of dark jaegers (Table 1, $t = 1.82$, $P = 0.034$, one-tailed test). The mixed chases are likely to have been initiated by a light bird half of the time. These results therefore accord well with the success of the chases of single jaegers. In the larger groups (3–6) differences in the same direction were found between the success of the all dark groups and the mixed groups (Table 1), although statistical significance was not found ($t = 0.79$, $P = 0.215$, one-tailed test), perhaps due to the small sample sizes.

Thus in this study area individuals of the rarer morph (light phase in this case) appeared to have greater hunting success than the more common ones, in agreement with the expectations of apostatic selection. However, when testing the apostatic selection hypothesis in field situations the success of the rare morph will always be

determined by a relatively small number of observations. The observations may therefore represent only one or a few individuals that happen to be particularly skillful hunters compared to the average of both the common and the rare morphs. It is therefore important to know how many different individuals are involved. Three distinct light-phased types of Parasitic Jaegers are recognizable in the field: (1) with a light breast and belly, (2) with a narrow dark band across the breast, and (3) with a broad dark band across the breast. Individuals of all three types were regularly seen at the cliff chasing puffins. I surveyed the area close to the puffin cliff for breeding pairs and found 12 light-phased individuals at nine nests and 35 dark-phased individuals at 22 nests. All of these probably hunted at the puffin cliff. Throughout the puffin-jaeger interaction period, and at different times of the day, I censused the numbers of jaegers patroling in a fixed volume of air at the puffin cliff (Arnason and Grant 1977). When present there were 1–3 (average = $1.3 \pm 0.5$ SD, N = 21) light-phased individuals seen at the cliff at any one time, whereas there were 3–20 dark-phased individuals per census (average = $7.1 \pm 3.1$ SD, N = 28). Thus the data in Table 1 represent no fewer than three and perhaps as many as 12 different light-phased individuals and as many 20 to 35 dark-phased individuals.

An average puffin encounters a jaeger approximately twice a week and loses its fish approximately once a week (Arnason and Grant 1977). Thus the puffins have ample reinforcement for learning a "parasite image." Approximately nine out of every 10 chases involve only dark-phased jaegers and the reinforcement for learning to recognize the dark phase as a threat is thus much greater than for the light phase.

The Parasitic Jaeger is best characterized as a maritime species (Pitelka et al. 1955) holding mating, nesting, and partly feeding territories in loose aggregations close to the sea. It obtains major parts of its food by kleptoparasitizing seabirds nesting close by (Arnason and Grant 1977). These resources are probably economically undefendable (Brown 1964) and the jaegers are not territorial on their kleptoparasitic feeding grounds. Parasitic Jaegers are important predators of eggs and young of the Pink-footed Goose (*Anser brachyrhyncos*), which nests in the interior of Iceland. There the jaegers apparently also do not hold typical all-purpose territories, but rather hunt in groups of 2–3 on communal hunting grounds (Sigurdsson 1974 and pers. comm., and see Maher 1974). Thus the two major problems of applying the hypothesis of apostatic selection to predators are alleviated in the case of the Parasitic Jaeger. On the other hand, the Pomarine and Long-tailed Jaegers (*S. pomarinus* and *S. longicaudus*), the former likewise polymorphic, have typical all-purpose territories (Pitelka et al. 1955), feeding mostly on rodents (Maher 1974, Anderson 1976b) within their territories. Apostatic selection is unlikely under these circumstances, as noted above. However, all three species of jaegers are kleptoparasites on their wintering grounds at sea and apostatic selection may play a role during winter.

If apostatic selection was the sole factor affecting the frequencies of two morphs one would expect to find a stable equilibrium at 0.5. Deviation of the equilibrium frequency from 0.5 would depend on the genetic system of the predator and the perceptual abilities of the prey (i.e. the relative ease with which the prey forms an image of the two morphs, c.f. Clarke 1964), as well as on the presence of frequency-independent selective forces affecting the system (Clarke and O'Donald 1964), such as those proposed by O'Donald and Davis (1975, and see also Anderson 1976a on suggestions of aggressive camouflage in jaegers). If the morph frequencies have reached equilibrium locally (wherever it may be), theoretical models predict that the two morphs should be equally successful at the point of balance. However, in nature

populations are finite and randomly drift away from the equilibrium. This creates selection back to the point of balance (the drift load, Kimura and Ohta 1971). Furthermore, the equilibrium gene frequencies may differ from the optimum phenotypic frequencies at which the fitness of the individuals is maximal (the dysmetric load, Kimura and Ohta 1971), creating additional selection. Clarke and O'Donald (1964) and Clarke (1964) have also shown that the presence of frequency-independent selective forces can lead to differential fitness at equilibrium. For these reasons we can expect selection to be operating most of the time. Proximately, we should therefore be able to measure differential hunting success of the two morphs at any locality and at any point in time, as was noted here for the Parasitic Jaeger.

The present observations accord with the prediction from the apostatic selection hypothesis. However, more data are needed to actually test the hypothesis. Data on the feeding efficiency of the two morphs of jaegers and avoidance responses of the puffins are needed from different populations from various parts of the jaegers' range. I therefore make a plea to Scandinavian workers to provide data from areas where the dark morph is rare and should be at an advantage, and to British workers, where the light-phased birds are rare and should be at a greater advantage than reported here, if apostatic selection indeed operates on the Parasitic Jaeger.

## LITERATURE CITED

ALLEN, J. A. 1976. Further evidence for apostatic selection by wild passerines—9:1 experiments. Heredity 36: 173–180.

———, & B. CLARKE. 1968. Evidence for apostatic selection by wild passerines. Nature 220: 501–502.

ANDERSON, M. 1976a. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118: 208–217.

———. 1976b. Ecology of long-tailed jaegers. J. Anim. Ecol. 45: 537–559.

ARNASON, E. 1974. Ecology and feeding behaviour of the Arctic Skua (Stercorarius parasiticus Linnaeus) in Iceland. Unpublished Master's thesis, Montreal, Canada, McGill Univ.

———, & P. R. GRANT. 1977. The significance of kleptoparasitism during the breeding season in a colony of Arctic Skuas Stercorarius parasiticus in Iceland. Ibis (in press).

BENGTSON, S.-A., & D. F. OWEN. 1973. Polymorphism in the Arctic Skua Stercorarius parasiticus in Iceland. Ibis 115: 87–92.

BERRY, R. J., & P. E. DAVIS. 1970. Polymorphism and behaviour in the Arctic Skua (Stercorarius parasiticus (L.)). Proc. Roy. Soc. Lond. B. 175: 255–267.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160–169.

CLARKE, B. 1962a. Balanced polymorphism and the diversity of sympatric species. In Taxonomy and Geography, (D. Nichols, Ed.). Oxford, England, Systematics Associations.

———. 1962b. Natural selection in mixed populations of two polymorphic snails. Heredity 17: 319–345.

———. 1964. Frequency-dependent selection for the dominance of rare polymorphic genes. Evolution 18: 364–369.

———. 1969. The evidence for apostatic selection. Heredity 24: 347–352.

———, & P. O'DONALD. 1964. Frequency-dependent selection. Heredity 19: 201–206.

DAWKINS, M. 1971. Perceptual changes in chicks: Another look at the "search image" concept. Anim. Behav. 19: 566–574.

GRANT, P. R. 1971. Interactive behaviour of Puffins (Fratercula arctica L.) and Skuas (Stercorarius parasiticus L.). Behaviour 40: 263–281.

———, & D. N. NETTLESHIP. 1971. Nesting habitat selection by Puffins (Fratercula arctica) in Iceland. Ornis Scand. 2: 81–87.

HILDÉN, O. 1971. Occurrence, migration and colour phases in the Arctic Skua (Stercorarius parasiticus) in Finland. Ann. Zool. Fennici 8: 223–230.

KIMURA, M., & T. OHTA. 1971. Theoretical aspects of population genetics. Princeton, New Jersey, Princeton Univ. Press.

KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus*). Behaviour Suppl. 11: 1–129.

MAHER, W. J. 1974. Ecology of Pomarine, Parasitic and Long-tailed Jaegers in Northern Alaska. Pacific Coast Avifauna, Number 37. Los Angeles, California, Cooper Ornithological Society.

O'DONALD, P., & 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.

PITELKA, F. A., P. Q. TOMICH, & G. W. TREICHEL. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Monogr. 25: 85–117.

SIGURDSSON, J. B. 1974. Rannsoknir a varphattum og afkomu heidagaesar. Skyrsla um rannsoknir i Thorsarverum 1972. Reykjavik, Iceland, Museum of Natural History.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. The principles and practice of statistics in biological research. San Francisco, Calif., W. H. Freeman.

SOUTHERN, H. N. 1943. The two phases of *Stercorarius parasiticus* (Linnaeus). Ibis 85: 443–485.

TINBERGEN, L. 1960. The natural control of insects in pinewood. I. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13: 265–336.

---

## ERRATA

The Proceedings of the 95th Stated Meeting of the American Ornithologists' Union [Auk 95 (1, Suppl.)] contains a resolution (number 7, page 11AA) considered by the Council but not presented to the General Session for adoption (see p. 5AA). Copies of those Resolutions adopted at the 95th Stated Meeting of the A.O.U. are available from the Secretary.

The caption for Table 1 in the article "Effect of cowbird parasitism on American Goldfinch nesting" (Auk 94: 304–307) is incorrect. The correct caption should read: "Comparison between clutch size and nesting success of parasitized vs. unparasitized and *un*parasitized adult goldfinches." Likewise, in columns 3 and 4, reference in both cases is to *un*parasitized nests.

---