

A PEREGRINE FALCON POLYMORPH: OBSERVATIONS OF THE REPRODUCTIVE BEHAVIOR OF *FALCO KREYENBORGI*

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ABSTRACT.—Observations of the reproductive behavior and productivity of the South American Pallid Falcon, historically known as Kleinschmidt's Falcon (*Falco kreyenborgi*), confirm and amplify findings by Ellis and Peres G. (1983), that *F. kreyenborgi* may be described in terms of a dichromatic polymorph of *F. peregrinus cassini*, the South American subspecies of Peregrine Falcon. The pallid form occurs relatively frequently in the eastern zone of the southern tip of South America, where it is locally sympatric with *F. p. cassini*. This study describes mating behavior of 17 pairs and productivity of 15 pairs of falcons in this region of southern Patagonia. In five of these pairs, both the adults were phenotypically "normal" *F. peregrinus*; in two pairs, both were pallid; and in ten pairs, the adults were mixed: a normal adult peregrine mated with a pallid individual. Phenotypic expression of the pallid trait from productivity data indicates that the genetic basis for pallidism is recessive to the normal genotype. My analysis of gene frequencies, based on this assumption, demonstrates a high frequency of heterozygosity among the local breeding population, which is characteristic of a clinal variation maintained by either low gene flow or selection for the pallid genotype.

The Pallid Falcon (*Falco kreyenborgi*) has been described as the rarest and the least known of the large falcons (Johnson 1972). Until recently, information about the Pallid Falcon had been limited to only a few recorded sightings and five collected specimens, three of which are of uncertain geographic origin (Hickey 1969). An historical review of the bird was given by Ellis et al. (1981). Owing mostly to its unusual coloration, *kreyenborgi*'s proper taxonomic placement has been the cause of considerable speculation (Kleinschmidt 1929, Peters 1931, Kovacs 1962-1963). Stresemann and Amadon (1963) showed that the Pallid Falcon's general morphological characteristics indicated a close association with *F. peregrinus cassini*, the South American subspecies of Peregrine Falcon. They concluded *kreyenborgi* might be a member of the Peregrine group. I conducted a study in order to investigate the distribution and breeding behavior of *F. kreyenborgi* with the intention of obtaining information necessary to determine its taxonomic placement in relation to *F. p. cassini*.

STUDY AREA AND METHODS

Between October 1980 and April 1982 I spent 16 months in southern Chile and Argentina (52-54°S, 68-73°W). During the 1980-1981 breeding season, I surveyed (primarily on foot and from automobile) large areas of the eastern foothills of the southern Andes in what Kuschel (1960) termed the "Magellanic moorland" and the lower "Magellanic forest." In the austral fall (March-April) of 1981, with the cooperation of the Chilean Servicio Agri-

cola y Ganadera, I established falcon trapping sites. During the 1981-1982 breeding season, I surveyed the eastern and relatively xeric Patagonian Steppe, including approximately 380 km of coastline. The data presented herein pertain exclusively to observations made during the 1981-1982 nesting season.

RESULTS

I located seventeen pairs of breeding falcons during the 1981-1982 nesting season in the eastern region of the province of Magallanes, Chile and the northern region of Tierra del Fuego. All but two eyries were situated along the Atlantic coast and the Straits of Magellan, and the remaining two were both within 40 km of the Straits.

Productivity data were obtained from 15 of the eyries located. Clutch sizes were mostly undetermined because I did not climb to the eyries until young were present. At two locations, however, the nests were observable from a distance enabling clutch size to be determined. I revisited the fifteen eyries at least once and no more than twice during the late nestling period (5 December-5 January). I climbed the eyrie cliffs, photographed young, and collected prey remains from the scrape. Prey species were identified from prey remains collected from the eyries and immediate vicinities and described in another paper (McNutt 1981). I considered young that had reached approximately four weeks of age to be successfully fledged. Plumage coloration was recorded for all adults and young, and individuals were described as either "normal" (*F.*

TABLE 1. Productivity and phenotype of adults and offspring at 17 Peregrine Falcon eyries in Chile and Tierra del Fuego in 1981-1982.

Eyrie no.	Parental phenotype		Productivity	Fledgling phenotype	
	Male	Female		Pallid	Normal
1	Normal	Normal	0	—	—
2	Normal	Normal	2	—	2
3	Normal	Normal	2	1	1
4	Normal	Normal	0	—	—
5	Normal	Normal	0	—	—
6	Normal	Pallid	2	2	—
7	Normal	Pallid	1	1	—
8	Normal	Pallid	U	—	—
9	Normal	Pallid	2	1	1
10	Normal	Pallid	1	1	—
11	Pallid	Normal	2	1	1
12	Pallid	Normal	2	2	—
13	Pallid	Normal	1	—	1
14	Pallid	Normal	2	1	1
15	Pallid	Normal	U	—	—
16	Pallid	Pallid	2	2	—
17	Pallid	Pallid	1	1	—

U = unknown.

peregrinus) or "pallid" (*kreyenborgi*) coloration. I considered two intermediately-colored offspring to be normal for the data analysis. The pallid plumage coloration is described, using Smithe's (1975) color guide, primarily based on colors recorded from an adult female trapped in April 1981.

Degree of paleness varied continuously among the pallid morphs that I saw, ranging from extremely pallid individuals to some which were heavily pigmented with dark markings. The pallid form was characterized by a pale cream-colored forehead; crown and nape pale cream, lightly flecked with dark neutral gray; the malar region defined by a few salmon-colored and blackish neutral flecks, and the rest of the face white; mantle, wing coverts, secondary remiges, and dorsal feathers basally light neutral gray gradually mixed with pale salmon, barred longitudinally with blackish neutral gray and tipped with white; tail coverts buff-yellow barred with blackish neutral gray to dusky brown distally; primaries dusky brown barred with salmon which changes laterally on the leading edge to dark neutral gray and white tips; tail mainly washed salmon (changing to medium neutral gray laterally) evenly barred with dusky brown and white at the tip; the under parts, including the flanks, breast, and under wing coverts, plain white with very slight thin fuscous bars visible in the flanks; the bill and talons whitish yellow at the bases fading to neutral gray at the tips. Darker pallid morphs had more conspicuous dusky brown and blackish neutral gray in all the blackish areas noted above and by Brown and Amadon (1968), including the tips of the talons and bill. The

TABLE 2. Summary of productivity data from Table 1.

Pair type	Breeding attempts	No. successful	Young fledged	Net productivity	Offspring	
					Normal	Pallid
Normal	5	2	4	0.8	3	1
Mixed	8	8	13	1.6	4	9
Pallid	2	2	3	1.5	0	3
Total	15	12	20	1.3	7	13

Net productivity is per breeding attempt.

crown and nape were darker neutral gray more conspicuously flecked with black; the malar region, which merged with an eye ring and continued dorsally into the occiput, more conspicuously flecked with black; dorsally darker neutral gray with only a hint of salmon color in otherwise pale neutral gray bars alternating with broader black bars; flanks, lower breast, and under wing coverts white with narrow dusky brown barring evident throughout, with the upper breast lightly flecked with fuscous. The general facial, head, and breast markings were found to be the most distinguishing characteristics in the field, emphasized by the white beneath and behind the eye and the overall absence of black in the head. I saw no adult falcon with coloration intermediate between the typical peregrine and the pallid plumages. Among the offspring, however, I saw two individuals (from two different nests) with what I called intermediate immature plumage. This plumage was characterized by a cinnamon-rufous coloration in the auricular region and the crown, plus cinnamon-rufous barring in a dusky brown tail, which resulted in a generally paler appearance than an otherwise normal peregrine.

In five of the seventeen pairs studied in 1981-1982, both adults were phenotypically normal. In ten pairs, one of the adults was a phenotypically peregrine and the other had typical pallid coloration. I saw two pairs in which both adults were pallid (Tables 1 and 2).

I determined clutch sizes at only two eyries, where eggs were counted from a distance. One contained two eggs, one of which was pushed or rolled out of the scrape late in the incubation period. The other contained three eggs, two of which were infertile. A third eyrie with one young also contained an infertile egg. All three of these eyries were of mixed pairs, i.e., a pallid morph mated with a phenotypically normal adult. All three successfully fledged one young.

Productivity data were not obtained from two eyries in which the adults were phenotypically mixed. Eight mixed pairs, representing 54% of all pairs from which productivity data were recorded, produced 69% (9) pallid offspring. The same eight pairs fledged four nor-

mal young. Of the five pairs of normal peregrines, only two (40%) successfully fledged young, producing an average of 0.8 young per breeding attempt. The cause of failure was undetermined. Two pairs of pallid adults produced 1.5 offspring per breeding attempt. Net productivity of mixed pairs was 1.6. All breeding attempts involving a pallid phenotype successfully fledged young.

DISCUSSION

The phenotype frequencies are $c:0.588$ and $k:0.412$, where c is normal *cassini* and k is pallid "*kreyenborgi*." Although there is a slight excess of mixed matings ($c \times k$: E = 8.24, O = 10) using the observed numbers of the three pair types from Table 2 (possibly because of the small sample size), I found no significant evidence that the two morphs were not mating at random. This, together with the apparent heritability of the phenotypes as indicated in the offspring phenotypes in Table 1, supports the view of Ellis and Peres G. (1983) that *F. kreyenborgi* should be regarded as a polymorph of *F. peregrinus cassini*. Bimodal or polymodal variation within a species is often referred to as polymorphism, which can be defined as "the occurrence together in the same habitat of two or more distinct genetic forms of a species of animal or plant in such proportions that the rarest of them cannot be maintained by recurrent mutation" (Ford 1940). Polymorphism is not uncommon in birds (Southern and Reeve 1941, Miller 1949, Mayr and Stresemann 1950, Cooch 1963, Mayr and Short 1970), and several instances are known in which a population or subspecies may be polymorphic whereas others of the same species are not; for example, Ruffed Grouse (*Bonasa umbellus*), Little Egret (*Egretta garzetta*), Sooty-capped Bush-Tanager (*Chlorospingus pileatus*). The Common Screech Owl (*Otus asio*), the eastern form of which is dimorphic whereas the western is not (Owen 1963), appears to be particularly analogous to the color variation observed in the South American peregrine.

There are two fundamental conditions of polymorphism (Ford 1940). "Transient polymorphism" may be said to be the continuous spreading of a favored gene. This assumes some unopposed selective agent or a favorable factor within the genetic mechanism itself (Southern and Reeve 1941), which ultimately results in displacement of the original allelomorph, and possibly complete speciation. The second possibility assumes that the spreading of the allelomorph has been checked by counter-selective forces resulting in a "balanced polymorphism" (Endler 1977). In a species

such as the Peregrine Falcon which has an extensive distribution but relatively small populations, it may be difficult or impossible to determine whether a form is presently transient, in terms of evolutionary time, and in the process of speciation, or if it is in a state of equilibrium with the normal morph. Parapatric contacts between species or "semi-species" in which reproductive isolating mechanisms either broke down or were never completely established are often considered secondary contacts between formerly allopatric populations (White 1978). However, in the case of the peregrine and "pallid falcon" in southeastern South America, I found no immediately plausible geographic or paleogeographic reason for believing that populations were ever geographically isolated. The lack of historical evidence that the two forms were ever isolated supports my view that, at some point in time, a selective advantage was conferred upon carriers of the k gene, enabling it to overcome the effects of genetic drift.

The apparent discreteness of the forms and the relative rarity of intermediates suggests that the trait is controlled by either a single locus or a group of loci so closely linked that they normally "behave" as if they were a single locus; i.e., with few exceptions, it is effectively inherited as a single unit. If we assume that the gene (or supergene) k is recessive to c , (as is suggested by pallid offspring being produced by normal adults), then the pallid phenotype is the result of the homozygous genotype kk , and the mixed matings would be either $cc \times kk$ or $ck \times kk$. In a $cc \times kk$ cross, all offspring would remain phenotypically normal falcons. Therefore, any normal morph involved in a reproductive attempt that produced a pallid offspring would necessarily be a heterozygous carrier of the recessive k gene. Every phenotypically mixed pair, except for one (Eyrie no. 13, Table 1), for which there is productivity data fledged at least one pallid offspring ($n = 7$, Table 1) ($n = 1$, Ellis and Peres G. 1983). The $ck \times kk$ cross is, therefore, the only genotype mating possibility for these mixed matings. The normal morphs that mated with a pallid, as well as any other normal pair that produced a pallid offspring (nine of 12 normal morphs which produced offspring, from Table 1), were genotypically heterozygous for both the c and k genes.

If the productivity data indicate the recessiveness of the k gene to c , then the gene frequencies from the adults which have determined genotypes ($n = 25$) are: $k = 0.74$, $c = 0.26$. One can assume that the low frequency of pallid morphs inland (0,0; $n = 12$; pers. obs.) and northward (0.046; $n = 22$; Ellis et al. 1981)

reflects a predominantly homozygous population of normal *F. peregrinus*. The existence, therefore, of a high proportion of heterozygotes probably represents a steep cline in morph ratios between the homozygous normal peregrine population and a potentially homozygous (*kk*) deme of pallid morphs. It is impossible to interpret a morph ratio cline without knowing the geography of differential viability (or fitness) or the extent of gene flow (Endler 1977). For example, the cline could be maintained by either a geographically defined high selection coefficient (superior viability) of the pallid morph and a constant gene flow, or moderate selection and a low rate of gene flow (Slatkin 1981). The fact that the two morphs appear to be mating at random suggests there is not presently a strong relative selection for the pallid morph over the normal morph (which includes the heterozygotes), as this should simultaneously select for assortative mating. It is possible that intense selection provided the mechanism for the original spreading of the pallid genotype at some time in the past. That pressure, however, does not necessarily still exist. Under relaxed selection, one could expect outbreeding or random mating of the morphs and a gradual flattening of the cline.

All of the nesting attempts that I found involving a pallid adult had a higher fledging success per attempt (100%) as well as higher productivity (1.5) than the pairs in which both adults were normal (40% and 0.8, respectively) (Table 2). This may reflect a higher absolute fitness of either the carriers of the *k* gene or specifically the *kk* homozygotes. The low fledging success of the five dark pairs is neither inconsistent with other figures for fledging success of *F. p. cassini* (Ellis, pers. comm.; McNutt, unpubl. data), nor for a few other peregrine populations in general (e.g., Hickey 1942, Cade and Fyfe 1970). The reason for the higher success ratio of the mixed pairs is unclear; it is not reflected, however, in the phenotype frequencies of the breeding adults. This may indicate a high rate of migration (gene flow) concurrent with a spatial selection gradient.

It is possible that mild selective agents which are not constant over distance are acting in favor of the pallid phenotype. These can be investigated qualitatively by analyzing *kreyenborgi*'s geographic distribution, breeding behavior, and productivity.

The precise geographic range of the pallid form is unknown, but the fact that the morph occurs with a higher frequency in the eastern part of the austral zone than in the western part indicates the existence of a non-random pattern of distribution. This might reflect the maintenance of the polymorphism by selec-

tion operating along environmental gradients. Distinct climatological gradients south of 52°S generally assume a northeast to southwest orientation, with a greater solar radiation (kcal/cm), greater average annual temperature, and less annual precipitation in the north and eastern zone (Zamora et al. 1981). Since the pallid form occurs in the relatively xeric zone of the austral region, it would be reasonable to speculate that climate is a selective factor favoring the pallid phenotype. These same climatological gradients continue northward and, north of 52°S, tend to assume an east-west orientation (Zamora, pers. comm.). If the warmer, drier climate selectively favors the pallid morph, we should expect to find higher frequencies of the pallid phenotype in the warmer, drier climates of northern and northeastern Patagonia. Complete censusing of Patagonia has not yet been undertaken, but Ellis et al. (1981), in a survey of central Patagonia, visited eleven Peregrine Falcon breeding sites and found only one adult "*kreyenborgi*." Ellis and Peres G. (1983), in a subsequent survey, reported five more adult pallid morphs involved in reproductive attempts in the Chubut and Santa Cruz provinces of Argentina. If these pallid morphs occurred specifically in the eastern zone of these provinces, it would further support the view that selection is operating along climatological gradients. However, since the distribution and frequency of these pallid morphs relative to the normal phenotype is not stated, it is difficult to say whether they coincide with climatological gradients. Interestingly, the majority of historical observations of the "Pallid Falcon" coincide with the observations described in this paper, which indicate a geographic distribution more concentrated in the extreme southeast region of Patagonia (Olrog 1948, Jehl and Rumboll 1976, Ellis and Glinski 1980). Recent observations of the pallid morphs may simply reflect a concentrated search for them. The possibility also exists, although there are few historical data, that Ellis's and Peres G.'s observations reflect an increase in the frequency of the pallid morph northward of 52°S.

Finally, the effects of random genetic drift must be considered as a possible means by which sympatric divergence could have occurred, particularly in light of the magnitude of these effects on small populations. Since the historical record of "*Falco kreyenborgi*" only reaches as far back as 1925 (at most thirty generations), it is conceivable that the persistence of the morph is solely the result of a neutrally selected genotype under the influence of genetic drift.

In future studies the geographic range and

frequencies of the pallid form of *F. p. cassini* throughout southern South America must be accurately delineated in order to clarify the relative magnitudes of the evolutionary processes acting upon it. Further observations of phenotype crosses in the breeding population, in conjunction with phenotype frequencies among offspring, are required to support the existence and illuminate characteristics of the morph ratio cline.

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