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Humans act against the natural process of breeder selection: a modern sickness for animal populations?

JAVIER BALBONTÍN*, VINCENZO PENTERIANI and MIGUEL FERRER
*Department of Applied Biology, Estación Biológica de Doñana, C.S.I.C., Avda. de María Luisa s/n., Pabellón del Perú, Apdo 1056, E-41013 Seville, Spain; *Author for correspondence (e-mail: balbonja@ebd.csic.es; fax: +34-95-5621125)*

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Abstract. We present a new idea about the possible effects of human-induced mortality on different age cohorts (i.e., breeders vs. juveniles) in long-lived animals. Our hypothesis is based on Curio's idea on the effect of natural selective processes on cohorts to explain age-related increases in fecundity (*selection hypothesis*). We believe that negative human pressure may modify such contribution to reproduction of good versus low quality phenotypes, altering the genetic structure of the population. Ecologists and environmental managers in general should be aware of how stochastic events provoked by humans may induce changes in the genetic structure of populations.

Introduction

Most bird species exhibit age-specific patterns of breeding performance: fecundity generally increases with age (Sæther 1983; Newton 1989; Desrochers and Magrath 1993; Forslund and Pärt 1995; Espie et al. 2000; Nielsen and Drachmann 2003) until senescence begins later in life (Newton 1981; Partridge 1989), increasing the probability of death (Watcher and Finch 1997). Among these studies, adults generally are more productive than youths and thus represent the main genetic contribution of a generation to the next one. Three hypotheses, not mutually exclusive, have been suggested to explain the above patterns that incorporate differences in individual quality among age classes, experience and reproductive cost (see reviews in Curio 1983; Forslund and Pärt 1995; Cam and Monnat 2000): (1) age-related improvements of competence (i.e., *constraint hypothesis*); (2) optimization of reproductive effort (i.e., *restraint hypothesis*); and (3) progressive appearance/disappearance of phenotypes (i.e., *selection hypothesis*). The *constraint hypothesis* proposes that age-related changes in competence during a bird's lifetime may improve skills that are essential to high reproductive performance, whereas the *restraint hypothesis* suggests that younger birds abstain from or put less effort into reproduction, because at that age reproductive effort increases mortality risk.

The *selection hypothesis* (Curio 1983) proposed that natural selection processes result in an age-related decrease in the proportion of lower-quality individuals in cohorts and consequently breeding success increases with age at the population level (Forslund and Pärt 1995; Cam and Monnat 2000). Actually, natural selection may remove lower-quality individuals at a higher rate from younger cohorts than from older ones, leading to a progressive increase of better quality phenotypes in the breeding age cohorts (Vaupel and Yashin 1985). This process of age cohort selection could explain age-related fecundity at the population level in most long-lived species (Cam and Monnat 2000), although several other factors may act in concert to increase reproductive performance with age (Nielsen and Drachmann 2003).

However, stochastic events such as human impact could change the proportion of high versus low quality individuals in cohorts, working against the selection of high-fitness individuals. In some cases, the strong site fidelity of breeders, their easy-to-detect aerial and vocal displays during the courtship period, as well as the increased frequency of activity during reproduction may facilitate the occurrence of human-induced mortality in adults, especially during reproduction. In this scenario, lower quality individuals generally belonging to the non-breeder cohorts have a higher probability of entering into the breeding population, probably lowering the overall quality of the genetic pool of the whole population.

Furthermore, even in those situations where adults and juveniles are equally exposed to the risk of anthropogenic mortality (e.g., poisoning, trapping or power line electrocution, which are stochastic events that can potentially affect with relatively similar probability floaters and breeders), the negative effects of human beings on mortality would be proportionally stronger on adult age-classes, since the natural process of individual selection is higher over the younger cohorts than over the older ones.

For example, a synthesis of the information on mortality rates in raptors (Table 1) highlights: (a) the higher survival of adults versus youngs; (b) that the differential in mortality rates between adults and youngs declines in the presence of mortality by humans (see *Accipiter gentilis*, *Falco mexicanus*, *Falco peregrinus*, *Haliaeetus leucocephalus*). The latter phenomenon, probably affecting a wide range of long-lived birds with deferred maturation (e.g., harvested species), can be more than ever evident for predators, particularly subject to mortality by human action, especially in places where they interfere with species of economic value (Thirgood et al. 2000).

The Bonelli's Eagle *Hieraaetus fasciatus* represents an example case of this situation. It is a threatened bird of prey that has suffered a dramatic decline in most areas of its European range and whose populations are nowadays mainly confined to the Iberian Peninsula and northern Africa (Real et al. 1996a; Arroyo et al. 1998). This long-lived species belongs to the group of species known as 'survival species' (Sæther et al. 1996), which are characterized by late age of first reproduction, low fecundity rate and high adult survival rate.

A long-term monitoring and radiotracking study has shown that human interference has recently lowered the adult survival rate, allowing non-adults to enter into the breeding population (Balbontín et al. 2003; Penteriani et al. 2003). Adult survival rate declined by approximately 5% due to human interference. Conversely, non-adult survival rate, measured by the monitoring of 30 radio-tagged non-adult eagles, was not affected (Balbontín et al. 2000). Besides, Real et al. (2001) recorded

Table 1. Mortality of young and adult birds of prey and owls. When available, data on populations in which both human-induced and natural mortality are acting are shown.

Species	Natural mortality		Natural + human-induced mortality		Source
	Juveniles	Adults	Juveniles	Adults	
Birds of prey					
Accipiter cooperii			80.5	39	Henny and Wight (1972)
A. gentilis			87	78	Höglund (1964)
	63	26			Haukioja and Haukioja (1970)
	58	38			Kramer (1973)
	64	26.5			Saurola (1976)
A. nisus	68	51			Tinbergen (1946)
	63	40			Schelde (1960)
	62	42			Kramer (1973)
	70	57			Newton (1975)
	66	32.5			Newton (1986)
	60	31			Newton (1986)
Aquila adalberti	84	6			Ferrer and Calderon (1990)
A. chrysaetos		7.5			Bezzel and Fünfstück (1994)
	70				PBRG (1995)
	85	5			Watson (1997)
A. verreauxi	55.7	8–9			Gargett (1990)
Buteo buteo	57	25			Olsson (1958)
	51	25.5			Mebs (1964)
B. jamaicensis	64.5	22.5			Henny and Wight (1972)
B. lineatus	58	31			Henny (1972)
Circus cyaneus		30			Hickey (1952)
	62	30			Watson (1977)
Falco columbarius		29			James et al. (1989)
F. mexicanus	74	25	67	45	Enderson (1969)
F. naumanni	34	29			Hiraldo et al. (1996)
F. peregrinus	70	25	50	30	Enderson (1969)
	71	19			Mebs (1971)
	56	28			Mebs (1971)
	59	32			Lindberg (1977)
	55	5			Olsen and Olsen (1988)
F. sparverius	65	49			Roest (1957)
	69	47			Henny (1972)
F. tinnunculus		44			Nordstrom (1963)
	50	35			Schifferli (1964)
	60	40.5			Snow (1968)
	68	34			Village (1990)
Gyps coprotheres	83	26			Piper et al. (1981)
Haliaeetus leucocephalus	95				Sherrod et al. (1977)
		6–8			Gerrad et al. (1992)
				12	Bowman et al. (1995)
	23.1	5.4			Jenkins (1996)
H. vocifer		4–6			Brown and Pommery (1984)
Hieraaetus fasciatus	9.9	90			Real et al. (1996b)
Milvus migrans		30			Schifferli (1967)
	56	27.1			Forero (1998)

Table 1. (Continued)

Species	Natural mortality		Natural + human-induced mortality		Source
	Juveniles	Adults	Juveniles	Adults	
Neophron percnopterus	11.2	10.3			Donázar et al. (2002)
Pandion haliaëtus	54.4	18.5–16.4			Henny and Wight (1969)
	56–60	78–82			Saurola (1983)
	51.5–57.3	16.2–18.5			Postupalski (1989)
Terathopius ecaudatus		3–6			Brown and Pommery (1984)
Owls					
Strix occidentalis	69.4	12.5			Thraikill et al. (1997)
Tyto alba	46.7	16.7			Henny (1969)
	65–75	30–40			Taylor (1994)

241 cases of death of Bonelli's Eagles between 1990 and 1998 in Spain, 38% of which were adults: a high mortality rate never detected until now. In addition, it was also reported in such a study that over 60% of adult breeders died on their breeding territory due to human persecution (Real et al. 2001). Game shooting activities seem to be directly associated with the majority of deaths in adult Bonelli's Eagle (Real et al. 2001).

The gradual removal of adult individuals, representing on average the high quality age cohorts, could be seen as a process acting in an antagonistic way against a natural process of selection. Thus, human persecution seems to act through a random or biologically unnatural elimination of individuals from the population, independently of their age and/or phenotype quality. It is well known that the relative strength of natural selection declines with the age of individuals (Hamilton 1966; Charlesworth 1994). Thus, if human interference affects either with the same or higher intensity the breeder cohorts, then the proportion of high versus low quality phenotypes is expected to change. Finally, the recently detected changes in the genotypic characteristics of several animal populations because of human-induced habitat modifications and direct anthropogenic stresses (e.g., Amos 1996; Baranyi et al. 1997; Reisenbichler 1997; Becher and Griffiths 1998; Gibbs 1998; Krane et al. 1999) seem to strongly support our hypothesis on the possible human-originating changes in the genetic structure of bird populations.

Human activities and their interference with natural processes have been claimed to be a pronounced modern problem for landscapes and animal populations, whose causes of extinction are often difficult to interpret. Actually, as stated by Moulton and Sanderson (1999) "with increasing frequency, we hear and read about mysterious decreases in or disappearances of living organisms". As in the case of Bonelli's Eagle and, more generally, when humans seem to act *unconsciously* against natural processes, we may wonder if we are now assisting and being confronted with a modern form of human-induced sickness, sapping the intrinsic and evolutionary stable structure of a population and reducing its probability of future survival.

We think that neglecting this aspect of human-induced mortality in animal populations could mean that we are ignoring an important aspect of their modern life history, and we hope that this brief report will encourage focusing the attention on the possible ecological and evolutionary changes that may occur under this scenario. The perception and awareness of such a negative interaction between natural processes and human activities may represent a useful conceptual framework for species conservation and management, and may help to avoid the repetition of the sad history of European and North American salmonids, for which the long-time interactions with human beings (e.g., harvest practices and domestication) resulted in changes of the life history traits and genetic pool that significantly impaired these species in ways that are still difficult to quantify (Ruckelshaus et al. 2002).

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