



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, 41013 Seville, Spain; *Author for correspondence (e-mail: balbonja@ebd.csic.es); fax: +34-95-5621125*

Received 11 February 2003; accepted in revised form 14 October 2003

Key words: Age cohorts, Bonelli's Eagle, Genetic structure of population, Human impact, Phenotypic quality, Selection hypothesis

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 hypothesis, 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*); and (2) optimization of reproductive effort (i.e., *restraint hypothesis*); (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 higher rate from younger cohorts than from older ones, leading to a progressive increase of better qualities 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 on 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), then 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 young; (b) that the differential in mortality rates between adults and young decline 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 *Hieraetus 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 decline by approximately 5% due to human interference. Conversely,

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

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

Table 1. (Continued)

Species	Natural mortality		Natural + human induced mortality		Source
	Juvenile	Adults	Juvenile	Adults	
<i>Neophron percnopterus</i>	11.2	10.3			Donázar et al. (in press)
<i>Pandion haliaëtus</i>	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)
<i>Terathopus ecaudatus</i>		3–6			Brown and Pommery (1984)
Owls					
<i>Strix occidentalis</i>	69.4	12.5			Thraikill et al. (1997)
<i>Tyto alba</i>	46.7	16.7			Henny (1969)
	65–75	30–40			Taylor (1994)

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 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 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 (Halmiton 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-originated 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 to 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).

Acknowledgements

S. Ormerod, J.L. Tella, I.G. Warkentin, F. Sergio and an anonymous referee made a useful critique to the first draft of the manuscript.

References

- Amos B. 1996. Levels of genetic variability in cetacean populations have probably changed little as a result of human activities. Report International Whaling Commission 46: 657–658.
- Arroyo B., Ferreiro E. and Garza V. 1998. Causas de la regresión del Águila Perdicera *Hieraetus fasciatus* en España Central. In: Chancellor R.D. Meyburg B.-U. and Ferrero J.J. (eds) Holarctic Birds of Prey. ADENEX-WWGBP, pp. 291–304.
- Balbotín J., Penteriani V. and Ferrer M. 2000. El águila perdicera en Andalucía: situación actual y tendencias en las áreas de reproducción y de dispersión juvenil. CSIC/Junta de Andalucía, Sevilla.
- Balbotín J., Penteriani V. and Ferrer M. 2003. Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's eagle in Andalusia. *Biological Conservation* 109: 417–423.
- Baranyi C., Gollman G. and Bobin M. 1997. Genetic and morphological variability in roach (*Rutilus rutilus*), from Austria. *Hydrobiologia* 350: 13–23.
- Becher S.A. and Griffiths R. 1998. Genetic differentiation among local populations of the European hedgehog (*Erinaceus europaeus*) in mosaic habitats. *Molecular Ecology* 7: 1599–1604.
- Bezzel E. and Fünfstück H.-J. 1994. Brutbiologie und Populationsdynamik des Steinadlers *Aquila chrysaetos* im Werdenfelser Land/Oberbayern. *Acta Ornithoecologica* 3: 5–32.
- Bowman T.D., Schempf P.F. and Bernatowicz J.A. 1995. Bald Eagle survival and population dynamics in Alaska after Exxon Valdez oil spill. *Journal of Wildlife Management* 59: 317–324.
- Brook B.W., O'Grady J.J., Chapman A.P., Burgman M.A., Akçakaya H.R. and Frankham R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404: 385–387.
- Brown L.H. and Pommery D.E. 1984. The age structure of populations of wild birds in tropical Africa as demonstrated by plumage characters and marking techniques. In: Proceedings of the V Pan-African Ornithological Congress, pp. 97–119.
- Cam E. and Monnat J.-Y. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology* 69: 380–394.
- Charlesworth B. 1994. *Evolution in Age-structure Populations*. 2nd edn. Cambridge University Press, Cambridge.

- Curio E. 1983. Why do young birds reproduce less well? *Ibis* 125: 400–404.
- Desrochers A. and Magrath R.D. 1993. Age-specific fecundity in European Blackbirds (*Turdus merula*): individual and population trends. *Auk* 110: 255–263.
- Donázar J.A., Palacios C.J., Gangoso L., Ceballos O., González M.J. and Hiraldo F. Conservation status and limiting factors in the endangered population of Egyptian vulture (*Neophron percnopterus*) in the Canary Islands. *Biological Conservation*.in-press.
- Enderson J.H. 1969. Peregrine and Prairie falcon life tables based on band-recovery data. In: Hickey J.J. (ed) *Peregrine Falcon Populations: Their Biology and Decline*. University of Wisconsin Press, Madison. pp. 505–508
- Espie R.H.M., Oliphant L.W., James P.C., Warkentin I.G. and Lieske D.J. 2000. Age-dependent breeding performance in Merlins (*Falco columbarius*). *Ecology* 81: 3404–3415.
- Ferrer M. and Calderón J. 1990. The Spanish Imperial Eagle (*Aquila adalberti*) in Doñana National Park: a study of population dynamics. *Biological Conservation* 51: 151–161.
- Forero G.M. 1998. Dispersión o filopatría? Análisis de sus causas y consecuencias en la población de milanos negros de Doñana. Ph.D. Dissertation, University of Seville, Spain.
- Forslund P. and Pärt T. 1995. Age and reproduction in birds – hypotheses and tests. *Trends in Ecology and Evolution* 10: 374–378.
- Gargett V. 1990. *The Black Eagle*. Acorn Books, Randburg, South Africa.
- Gerrad J.M., Gerrad P.N., Bortolotti G.R. and Dzus E.H. 1992. A 24-year study of Bald Eagles on Besnard Lake, Saskatchewan. *Journal of Raptor Research* 26: 159–166.
- Gibbs J. 1998. Genetic structure of redback salamander *Plethodon cinereus* populations in continuous and fragmented forests. *Biological Conservation* 86: 77–81.
- Halmiton W.D. 1966. The molding of senescence by natural selection. *Journal of Theoretical Biology* 12: 12–45.
- Haukioja E. and Haukioja M. 1970. Mortality rates of Finnish and Swedish Goshawks (*Accipiter gentilis*). *Finnish Game Research* 31: 13–20.
- Henny C.J. 1969. Geographical variation in mortality rates and production requirements of the barn owl (*Tyto alba*). *Bird-Banding* 40: 277–356.
- Henny C.J. 1972. An analysis of the population dynamics of selected avian species. Bureau Sport Fisheries and Wildlife, Res. Rep. 1. Washington, DC.
- Henny C.J. and Wight H.M. 1969. An endangered Osprey population: estimates of mortality and production. *Auk* 86: 188–198.
- Henny C.J. and Wight H.M. 1972. Red-tailed and Cooper's Hawks: their population ecology and environmental pollution. In: *Population Ecology of Migratory Birds*. Symposium Volume, Patuxent Wildlife Research Center, pp. 229–250
- Hickey J.J. 1952. Survival studies of banded birds. US Dept. Int. Spec. Sci. Rep. Wildlife 15.
- Hiraldo F., Negro J.J., Donázar J.A. and Gaona P. 1996. A demographic model for a population of the endangered lesser kestrel in southern Spain. *Journal of Applied Ecology* 33: 1085–1093.
- Höglund N. 1964. Der Habicht *Accipiter gentilis* Linné in Fennoscandia. *Viltrevy* 2: 195–270.
- James P.C., Warkentin I.G. and Oliphant L.W. 1989. Turnover and dispersal in urban merlins *Falco columbarius*. *Ibis* 131: 426–447.
- Jenkins J.M. 1996. Modelling of a resident Bald Eagle *Haliaeetus leucocephalus* population using empirical life table parameters. In: Meyburg B.-U and Chancellor R.D. (eds) *Eagles Studies*. WWGBP, Berlin. pp. 189–198.
- Kramer K. 1973. *Habicht und Sperber*. Die Neue Brehm-Bücherei. Ziemsen Verlag. Wittenberg Lutherstadt.
- Krane D.E., Sternberg D.C. and Burton G.A. 1999. Randomly amplified polymorphic DNA profile-based measures of genetic diversity in crayfish correlated with environmental impacts. *Environmental Toxicology and Chemistry* 18: 504–508.
- Lindberg P. 1977. The Peregrine Falcon in Sweden. In: *Proc. ICBP World Conference on Birds of Prey*, Vienna, pp. 329–338.
- Mebs T. 1964. Zur Biologie und Populationsdynamik des Mäusebussards *Buteo buteo*. *Journal für Ornithologie* 105: 247–306.

- Mebs T. 1971. Death causes and mortality rates of Peregrines *Falco peregrinus* calculated by German and Finnish band-recoveries. *Die Vogelwarte* 26: 98–105.
- Meffe G.K. and Carrol C.R. (eds) 1994. *Principles of Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Moulton M.P. and Sanderson J. 1999. *Wildlife Issues in a Changing World*. CRC Press, Boca Raton, FL, USA.
- Newton I. 1975. Movements and mortality of British Sparrowhawks. *Bird Study* 22: 35–43.
- Newton I. 1981. Age and breeding in Sparrowhawks. *Journal of Animal Ecology* 50: 839–853.
- Newton I. 1986. The Sparrowhawk. T and AD Poyser, Calton.
- Newton I. (ed) 1989. *Lifetime Reproduction in Birds*. Academic Press, London.
- Nielsen J.T. and Drachmann J. 2003. Age-dependent reproductive performance in Northern Goshawks *Accipiter gentilis*. *Ibis* 145: 1–8.
- Nordstrom G. 1963. Einige Ergebnisse der Vogelberingung in Finnland in der Jahren 1913–1962. *Ornis Fennica* 40: 81–124.
- Olsen P.D. and Olsen J. 1988. Population trends, distribution, and status of the Peregrine Falcon in Australia. In: Cade T.J., Enderson J.H., Thelander C.J. and White C.M. (eds) *Peregrine Falcon Populations*, The Peregrine Fund, Inc., Boise, ID, pp. 255–287.
- Olsson O. 1958. Dispersal, migration, longevity and death causes of *Strix aluco*, *Buteo buteo*, *Ardea cinerea* and *Larus argentatus*. *Acta Vertebratica* 1: 91–189.
- Partridge L. 1989. Lifetime reproductive success and life-history evolution. In: Newton, I. (ed). *Lifetime Reproduction in Birds*. Academic Press, London, pp. 421–440.
- PBRG (Predatory Bird Research Group). 1995. A pilot Golden Eagle population study in the Altamont Pass Wind Resource Area, California. University of California, Santa Cruz.
- Penteriani V., Balbontín J. and Ferrer M. 2003. Simultaneous effects of age and territory quality on fecundity in Bonelli's Eagle (*Hieraetus fasciatus*). *Ibis*, 145: E77–E82.
- Piper S.E., Mundy P.J. and Ledger J.A. 1981. Estimates of survival in the Cape Vulture *Gyps coprotheres*. *Journal of Animal Ecology* 50: 815–825.
- Postupalski S. 1989. *Osprey*. In: Newton I. (ed) *Lifetime Reproduction in Birds*. Academic Press, London, pp. 297–313.
- Primack R.B. 1994. *Essentials of Conservation Biology*. Sinauer Associates, Sunderland, MA.
- Real J., Mañosa S. and Codina J. 1996a. Estatus, demografía y conservación del Aguila perdicera *Hieraetus fasciatus* en el Mediterráneo. In: Muntaner J. and Mayol J. (eds) *Biología y Conservación de las Rapaces Mediterráneas*, Monografía No. 4, SEO, pp. 83–89.
- Real J., Mañosa S., Cheylan G., Bayle P., Cugnasse J.M., Sánchez-Zapata J.A. 1996b. A preliminary demographic approach to the Bonelli's Eagle *Hieraetus fasciatus* population decline in Spain and France. In: *Eagles Studies*. Meyburg B.-U. and Chancellor R.D. (eds) WWGBP, Berlin, pp. 523–528.
- Real J., Grande J.M., Mañosa S. and Sánchez-Zapata J.A. 2001. Geographic variation of the causes of death of Bonelli's Eagle (*Hieraetus fasciatus*) in Spain. *Bird Study* 48: 221–228.
- Reisenbichler R.R. 1997. Genetic factors contributing to declines of anadromous salmonids in the Pacific Northwest. In: Naiman R.J. (ed) *Pacific Salmon and Their Ecosystems: Status and Future Options*. Chapman & Hall, New York, NY, USA, pp. 223–244.
- Roest A.I. 1957. Notes on the American Sparrowhawk. *Auk* 74: 1–19.
- Ruckelshaus M.H., Levin P., Johnson J.B. and Kareiva P.M. 2002. The Pacific Salmon Wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33: 665–706.
- Sæther B.E. 1983. Age-specific variation in reproductive performance of birds. In: Power D.M. (ed) *Current Ornithology*, Vol. 7. Plenum Press, New York, pp. 251–283.
- Sæther B.-E., Ringsby T.H. and Roskaft E. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77: 217–226.
- Saurola P. 1976. Mortality of Finnish Goshawks. *Suomen Luonto* 6: 310–314.
- Saurola P. 1983. Population dynamics of the Osprey in Finland during 1971–1980. In: *Biology and Management of Bald Eagles and Ospreys*. Bird D.M. (ed) Harpell Press, Ste. Anne de Bellevue, Quebec, pp. 201–206.

- Schelde O. 1960. The migration of Danish Sparrowhawks (*Accipiter nisus*) L. Dansk Orn. For. Tidssk 54: 88–102.
- Schifferli A. 1964. Lebensdauer, Sterblichkeit und Todesursachen beim Turmfalken, *Falco tinnunculus*. Ornithologische Beobachter 61: 81–89.
- Schifferli A. 1967. Vom Zug Schweizerischer und Deutscher Schwarzer Milane nach Ringfunden. Ornithologische Beobachter 64: 34–51.
- Sherrod S.K., White C.M. and Williamson F.S.L. 1977. Biology of the Bald Eagle on Amchitka Island, Alaska. Living Bird 15: 143–182.
- Snow D.W. 1968. Movements and mortality of British Kestrels *Falco tinnunculus*. Bird Study 15: 65–83.
- Steenhof K., Kochert M.N. and Doremus J.H. 1983. Nesting of subadult Golden Eagles in southwestern Idaho. Auk 100: 743–747.
- Taylor I. 1994. Barn Owls. Predator–Prey Relationships and Conservation. Cambridge University Press, Cambridge.
- Thirgood S., Redpath S., Newton I. and Hudson P. 2000. Raptors and Red grouse: conservation conflicts and management solutions. Conservation Biology 14 1: 95–104.
- Thraikill J.A., Anthony R.G. and Meslow E.C. 1997. An update of demographic estimates for northern spotted owls *Strix occidentalis caurina* from Oregon's Central Coast Ranges. In: Duncan J.R., Johnson D.H. and Nicholls T.H. (eds) Biology and Conservation of Owls of the Northern Hemisphere. USDA Forest Service, General Technical Report NC-190, St. Paul, MN.
- Tinbergen L. 1946. Sperver als Roofvijand van Zangvogels. Ardea 34: 1–123.
- Vaupel J.W. and Yashin A.I. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. American Statistician 39: 176–185.
- Village A. 1990. The Kestrel. T and AD Poyser, London.
- Wachter K.W. and Finch C.E. 1997. Between Zeus and the Salmon. The Biodemography of Longevity. National Academy Press, Washington, DC.
- Watson D. 1977. The Hen Harrier. T and AD Poyser, Berkhamsted.
- Watson J. 1997. The Golden Eagle. T and AD Poyser, London.
- Weimerskirch H. and Jouventin P. 1987. Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Island: causes and consequences of the population decline. Oikos 49: 315–322.
- Wilson E.O. (ed) 1988. Biodiversity. National Academy Press, Washington. DC.