Saari, L. 1977: Change of habitat preference during the summer in certain passerines. — Ornis Fennica 54:154–159.
Solonen, T. 1985: Suomen linnusto. — Lintutieto, Helsinki.
Sonerud, G. A. & Bekken, J. 1979: Vierspurvens utbredelse i Norge og dens habitatvalj i Hedmark. — Vår Fuglefauna 2:78–85.
Staav, R. 1976: Videsparven i Sverige, utbredning och uppträdande under flyttningen. — Fauna och Flora 71:202–207.
Tiainen, J. 1988: Ornitologian menetelmät 5. Lintujen pesimistuloksen arvioiminen Mayfieldin menetelmällä. — Ornis Fennica 65:122–124.
Ukkonen, M. 1983a: Pohjansirkku Emberiza rustica. — In: Hyytiä, K., Kellomäki, E. & Koistinen, J. (eds): Suomen lintuatlas, pp. 474–475. Lintutieto, Helsinki.
Ukkonen, M. 1983b: Pohjansirkun (Emberiza rustica) pesimäbiologiasta. — Unpublished M. Sc. Thesis, University of Helsinki, Dept. of Zoology, 210 pp.
Ukkonen, M. 1983c: Milloin pohjansirkku pesii. — Siivekäs 4:117–122.

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Poor predictability of the threatened status of waterfowl by life-history traits

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Twenty of the (about) 149 waterfowl (Anatidae) species in the world (Johnsgard 1978) are considered threatened or recently extinct (Collar & Andrew 1988). A recent collation of demographical and other data on the waterfowl of the world (Laurila 1988) makes it possible to examine whether the threatened waterfowl form a subset that deviates from the common waterfowl pattern. Threatened waterfowl species might be expected to share some features that make them especially prone to decline in numbers, e.g. late age at maturity, small clutches or long breeding periods. As the data are not sufficient for the inclusion of many variables, we are limited to the basic life-history traits reported in the literature. Even so, we have to exclude seven species because of insufficient data, and one threatened species (the Freckled Duck *Stictonetta naevosa*) because it is the sole representative of its tribe. Owing to differences between the classifications by Johnsgard (1978, used by Laurila 1988) and Collar & Andrew (1988, used by us), the data for the Hawaiian Duck *Anas wyvilliana* and the Laysan Duck *A. laysanensis* are added here.

Four of the seven species excluded because of scanty data were threatened (Crested Shelduck *Tadorna cristata*, Madagascar Teal *Anas bernieri*, Brazilian Merganser *Mergus octosetaceus* and Scaly-sided Merganser *M. squamatus*). This reflects the fact that little attention is paid to species having restricted ranges in remote corners of the world. This is also true of a fifth omitted species, the Labrador Duck *Camptorhynchus labradorius*, extinct since the 19th century.

Table 1 shows the ranges of reproductive parameters for threatened and other waterfowl. No marked differences are evident (the narrower ranges among the threatened species are most probably a statistical consequence of the smaller sample size). This observation may, however, be misleading, as size and phylogeny were found to explain 30–90% of the between-species variation in reproductive traits (clutch size, incubation period, egg size, time required for breeding) in waterfowl (Laurila 1988). Larger species mature later and have smaller clutches than small species. Also, all true geese (Anserini) are "poor reproducers" compared with ducks (Anatini), as the former mature later and have smaller clutches in relation to their size (Laurila 1988). We therefore compared the reproductive traits of each threatened spe-

Table 1. Ranges of the reproductive parameters and size of 15 threatened and 129 other waterfowl species.

	Threatened	Other
Female weight (kg)	0.4–2	0.2–10
Clutch size	5–11	2–14
Egg weight (g)	31–144	23–340
Incubation period (d)	25–31	22–43
Time required for breeding (d)	71–119	66–207

Table 2. Phylogeny and general biology of the 13 threatened waterfowl species included in the analysis. The following abbreviations are used. Paternal care (*PC*): P = present, A = absent. Feeding system (*FS*): DG = dabbling or grazing, DA = dabbling, DI = diving. Mating system (*MS*): MP = monogamous, permanent pair-bond, MG = monogamous, seasonal pair bond, PG = polygamous. Nest concealment (*NC*): P = present, A = absent, H = holes or cavities.

Species	Tribe	*PC*	*FS*	*MS*	*NC*
Dendrocygna arborea	Dendrogygnini	P	DG	MP	P
Anser erythropus	Anserini	P	DG	MP	A
Branta sandvicensis	Anserini	P	DG	MP	A
B. ruficollis	Anserini	P	DG	MP	A
Chloephaga rubidiceps	Tadornini	P	DG	MP	P
Cairina scutulata	Cairinini	A	DA	PG	H
Anas formosa	Anatini	A	DA	MG	P
A. aucklandica	Anatini	P	DG	MP	?
A. wyvilliana	Anatini	?	DA	?	P
A. laysanensis	Anatini	?	DA	MG	P
Marmaronetta angustirostris	Anatini	A	DA	MG	P
Rhodonessa caryophyllacea	Aythyini	?	DA	?	P
Aythya baeri	Aythyini	A	DI	MG	P
A. innotata	Aythyini	A	DI	MG	A
Oxyura leucocephala	Oxyurini	A	DI	MG	P

Table 3. Reproductive traits and distribution of the 15 threatened species included in the analysis compared with the mean values for their tribes (see Laurila 1988). The numbers indicate how many species have a value greater than, equal to or smaller than the tribe mean. When the sum of species is less than 15, a number of species have been omitted owing to missing data. Only the figures for the breeding range differ significantly (binomial P<0.001) from the expected 1:1 distribution of greater and smaller values.

	Greater	Equal	Smaller
Female weight	5	–	10
Age at fledging	4	1	3
Incubation period	9	4	2
Clutch size	5	4	6
Age at maturity	1	8	2
Egg weight	6	–	9
Distance from equator	7	–	8
Breeding range	–	–	15

cies with the mean values of its tribe. (In another analysis, not reported here, we included the six "near-threatened" species listed by Collar & Andrew (1988), but their inclusion did not alter the present results.)

There was no tendency for threatened species to be large (Tables 1 and 3), nor were they concentrated in one tribe (Table 2), nor did they have consistent similarities in their biology (Table 2). When compared with other species of the same tribe, the threatened species showed no special differences in reproductive traits (Table 3).

The one trait the threatened species invariably had in common was a restricted range (Table 3; this also applies to species omitted because of insufficient data). This fact can be interpreted in two ways. On the one hand, it may mean that being threatened implies being restricted in range, so that the result is more or less tautological. On the other hand, none of the threatened species is known to have had a wide range before the populations were significantly affected by human activity. For example, seven of the twenty threatened species are insular. We interpret this as showing that restricted ranges are in fact a cause of the threatened status, not merely its consequence. This finding echoes the conclusion by Terborgh & Winter (1980), who concluded that "rarity proves to be the best index of vulnerability" (but see Simberloff 1986 for a critical discussion of the term "rarity"). Rarity is not the only cause, however: there are species that are known to have had wide ranges, but that have nevertheless gone extinct, such as the Passenger Pigeon *Ectopistes migratorius*.

It seems reasonable to assume that the human impact on a population can most easily bring it (close) to extinction when the geographical range is restricted, even if the species is abundant within its range. As there is no doubt that extinctions in the world of today are almost exclusively human-related, it follows that a restricted geographical range is quite generally a correlate of extinction-proneness. However, this does not answer a more fundamental question in ecological zoogeography, which has deep implications for conservation biology: what are the species likely to decline so radically that their ranges will collapse critically? In their study of bird species turnover in Northern Europe in 1850–1970, Järvinen & Ulfstrand (1980) concluded that most extinctions were related to persecution (incl. hunting) and habitat changes; many of the disappearing species were habitat specialists, and tropical migrants were more likely to disappear from Northern Europe than intra-Palearctic migrants, whereas large size (associated with demographic parameters) was not a very good predictor of extinction probability.

Why then are demographic traits poor predictors of threatened status? It is known that demographical traits may indeed make a species vulnerable: slowly reproducing, long-lived species suffer from remarkably small increases in adult mortality (Mertz 1971, Järvinen & Varvio 1986). Waterfowl, hunted extensively in most parts of the world, could thus be expected to include taxa in which demographic traits correlate with extinction risks. The fact that this is not the case indicates that hunting is by no means the greatest threat to natural waterfowl populations (see also Simberloff 1986). Indeed, it is evident from the literature (Johnsgard 1978, Collar & Andrews 1988) that in many cases indirect human influence, such as habitat alteration or introduced species, with or without direct persecution, has been effective in decimating the waterfowl species that are now threatened.

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Selostus: **Onko uhatuilla sorsalintulajeilla yhteisiä piirteitä?**

Maailman 149 sorsalinnusta luokitellaan 20 uhatuiksi. Laurilan (1988) kokoamien sorsalintujen lisääntymisbiologisten tietojen avulla vertasimme uhattujen lajien tietoja niiden lähisukulaisten keskiarvoihin.

Uhatut lajit eivät edustaneet selvästi mitään ryhmää (esim. pitkäikäisimpiä sukuja). Uhattujen lajien koko ja elintavat vaihtelivat yhtä paljon kuin sorsalintujen yleensä (taul. 1). Lähisukulaisiinsa verrattuina uhattujen lajien lisääntymisominaisuudet olivat yhtä usein parempia kuin huonompia (taul. 2–3). Ainoa uhattujen lajien selvästi yhteinen piirre oli suppea maantieteellinen levinneisyys. Tämä on hyvin ymmärrettävää, sillä suorat tai epäsuorat ihmisvaikutukset ovat tehokkaimpia (ja tuhoisimpia) silloin, kun lajin levinneisyysalue on suppea.

References

Collar, N. J. & Andrew, P. 1988: Birds to watch. The ICBP world checklist of threatened birds. — ICBP Tech. Publ. 8, Cambridge, 320 pp.

Järvinen, O. & Ulfstrand, S. 1980: Species turnover of a continental bird fauna: Northern Europe, 1850–1970. — Oecologias (Berl.) 46:186–195.

Järvinen, O. & Varvio, S.-L. 1986: Proneness to extinction of small populations of seals: demographic and genetic stochasticity vs. environmental stress. — Finnish Game Res. 44:6–18.

Johnsgard, P. 1978: Ducks, geese and swans of the world. — Univ. Nebraska Press, Lincoln, 404 pp.

Laurila, T. 1988: Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size and phylogeny. — Ornis Fennica 65:49–64.

Mertz, D. B. 1971: The mathematical demography of the California Condor population. — Amer. Nat. 105:437–454.

Simberloff, D. 1986: The proximate causes of extinction. — In: Raup, D. M. & Jablonski, D. (eds.), Patterns and processes in the history of life, pp. 259–276. Springer, Berlin.

Terborgh, J. & Winter, B. 1980: Some causes of extinction. — In: Soulé, M. E. & Wilcox, B. A. (eds.), Conservation biology. An evolutionary-ecological perspective, pp. 119–133. Sinauer, Sunderland, Mass.

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Blue Tit *Parus caeruleus* and Pied Flycatcher *Ficedula hypoleuca* breeding simultaneously in a nest box

Aarno Magnusson

An unusual drama took place in one of the nest boxes belonging to Tiirankari Bird Station (60°15′N, 23°57′E) in 1989. The area is a mixed forest along the northern shore of Lake Lohjanjärvi in SW Finland.

During a routine check on 1 June 1989 I found that the nest box contained a finished nest of the Blue Tit, but no eggs. The Blue Tit fought hard with a male Pied Flycatcher. The female Pied Flycatcher was also present.

On 3 June there was one Blue Tit egg and one of the Pied Flycatcher. The eggs were not covered by nest material as normally with tits. All inspections took place between 1000 and 1300 hours. The following day there were two uncovered eggs of both species. On 6 June there were three eggs of the Pied Flycatcher and four of the Blue Tit. The eggs were covered. On 7 June there were still three Flycatcher eggs, but five Blue Tit eggs, the eggs not covered. For