Ecological factors and human threats both drive wildfowl population declines

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Abstract

Many wildfowl species are declining and 34 out of 159 extant species are globally threatened, some of which are the subject of specific conservation programmes. Here we investigate which factors predict declining population trends across 154 species of Anseriformes. First we show that there are proportionately fewer declining wildfowl populations in North America, Europe and Australasia than in south and central America, Africa and Asia. Second, we use phylogenetic comparative analyses to test whether population size, global range size and ecological, life-history and sexually-selected traits predict population trends. We also consider anthropogenic threats, and human impacts within the breeding and non-breeding ranges of species. Using phylogenetically independent contrasts we show that small population size and small global ranges are the most important intrinsic factors that predispose wildfowl species to declining populations. Many wildfowl are hunted but, contrary to expectation, hunting did not influence population trends. Declining populations were associated with high International Union for the Conservation of Nature (IUCN) threat category, although the relationship is not very strong ($r = 0.134$, $n = 129$ contrasts) possibly because the IUCN criteria integrate population size, range size and an assessment of threat. Two extrinsic factors were significant predictors of population declines: the increase in area of agricultural land within a species' range (an indirect measure of wetland loss), and the total number of different threat processes such as habitat loss and pollution that threaten a species. Taken together, our results strongly suggest that both anthropogenic threats and intrinsic ecological factors are influencing population declines in wildfowl.

Introduction

Globally, many of the 159 species of Anseriformes (ducks, geese, swans and screamers) are declining and 21% of these are currently threatened with extinction (Wetlands International, 2002). Extinction risk within avian taxa is not randomly distributed (Bennett & Owens, 1997). Across all birds several candidate factors have been identified to explain these extinction risk patterns; range sizes (Blackburn & Gaston, 2002); ecological traits such as habitat elevation (Gage et al., 2004); life-history traits such as large body size and small clutch size (Arnold & Owens, 2002) and sexually selected traits such as large relative testes mass (Morrow & Pitcher, 2003).

Fisher & Owens (2004) argue that although taxonomically broad studies are effective in determining general correlates of extinction risk, studies which focus on a smaller taxonomic group will be more effective in identifying interactions between intrinsic and extrinsic factors responsible for population declines. In this paper we use wildfowl, a group that shows considerable diversity in ecology, life-history and habitat use to investigate the influence of these factors on population trend over time.

Anseriformes are excellent indicator species for the health of wetlands (Furness & Greenwood, 1993). Wetlands are highly productive, diverse globally distributed ecosystems, but are threatened by a number of processes including drainage and conversion to agricultural land, over-harvesting of natural resources, changes to the hydrological regime, pollution and invasive species (Moser et al., 1996).

Both intrinsic (i.e. ecological and life-history) and extrinsic (i.e. human-induced) effects may be involved in population declines. First, a species' population size and range size are likely to be important predictors of population trend as small populations will be more threatened due to demographic stochasticity, the risk of catastrophes and inbreeding (Gaston, 1994; Simberloff, 1998; Briskie & Mackintosh, 2004). Of course, it is possible that small population size and ranges are emergent properties of declining populations, but it is not possible for us to test this causality.

Second, species at higher trophic levels – higher up the food chain – may be expected to have a more adverse

population trend than species at a lower trophic level at a given level of anthropogenic pressure as a result of vulnerability to 'chains of extinction' effects (Diamond, 1984), and the need for lower population densities. Migratory species may be more threatened as a result of high site fidelity and dependence on two separate areas in which they may be at risk from anthropogenic changes to the landscape (Pimm, Jones & Diamond, 1988). However a migratory habit may also confer greater dispersal ability and adaptability to different environments, which may buffer the species from other threats (Green, 1996).

Third, life-history traits such as large body size, small clutch size, delayed sexual maturity, which are associated with more K-selected slow life-histories, may predispose a species to decline (Pimm *et al.*, 1988; Gaston & Blackburn, 1995). This results from a decreased ability to increase fecundity to compensate for increases in adult mortality in the population.

Fourth, intense sexual selection is considered to increase extinction risk (Moller, 2000). Kokko & Brooks (2003) argue that strong sexual selection causes species to evolve traits which increase mating opportunities, but at a fitness cost which compromises survival. Morrow & Pitcher (2003) found that only post-mating sexual selection (sperm-competition) is correlated with increased extinction risk in birds, and that pre-mating sexual selection is not associated with elevated threat status.

Finally, humans may threaten a species in a variety of ways, such as habitat modification, hunting and introducing alien species to an ecosystem. Unfortunately, it is difficult in most cases to directly measure human impacts on a species. Instead, one may identify indices of human activity, which coincide in space and time with the population trend in the species of interest. Thus, *proxy* measures such as human population density within each species range were used. Cardillo *et al.* (2004) found human population density within carnivore ranges predict conservation status. However, other measures of human impact such as number of households (Liu *et al.*, 2003) may be more suitable.

Green (1996) examined the impacts of intrinsic and extrinsic factors on wildfowl, but without controlling for the effects of phylogeny. It is not appropriate to treat values of traits from closely related species as independent since such traits are often shared through common descent rather than independent evolution. Phylogenetic comparative methods allow comparisons to be made by examining independent evolutionary events. Other workers have considered the effects of phylogeny, but have not incorporated extrinsic factors into their analyses of threatened wildfowl (Gaston & Blackburn, 1996). Furthermore, almost all previous studies of factors affecting the conservation status of a taxon have adopted International Union for the Conservation of Nature (IUCN) categories ('Red Lists', ranging from extinct to least concern) as a response variable. Unless this effect is controlled for by excluding species listed under the criteria from certain analyses, this can introduce the problem of logical circularity into any analysis of whether factors such as range size explain variations in conservation

status, as population size, rate of decline and range size have been used to derive the IUCN categories (IUCN, 2001).

In order to avoid this potential pitfall, we use population trend as our response variable. Population trend is an emergent property of natural populations that may be observed (Kunin & Gaston, 1997). We argue that population trend is a more independent measure of conservation status than IUCN categories. However, it is important to note that population trend, unlike the IUCN categories, does not necessarily equate to extinction risk. It is possible for a large population to have a slowly decreasing trend yet not have its persistence seriously threatened. Conversely, in extreme circumstances it is possible for a species assessed by IUCN criteria to be highly threatened, to have a stable or even increasing population trend, although only if its population size was lower than the threshold for listing in an IUCN category under criterion D (population size).

In this study we use phylogenetic comparative analyses to identify the factors that make some wildfowl species more threatened than others. We ask how intrinsic aspects of a species' biology and extrinsic human influences within a species' range contribute to the population trend of wildfowl. We assess the relative importance of population size and range, ecological traits, life-history traits and sexually selected traits. We also consider anthropogenic threat processes, and human impacts in the global range of each species. In addition, we test whether intrinsic biological traits make species more susceptible to extrinsic threats. Duncan, Blackburn & Worthy (2002) explored this interaction in relation to island birds, here we apply this approach across an order of birds.

Methods

We used data from Waterbird Population Estimates (WPE, Wetlands International, 2002) on population size and population trend of 458 populations of 161 species of ducks, geese, swans and screamers (Anseriformes) as listed in Monroe & Sibley (1993). Bird handbooks were the major sources for the database of ecological, life-history and sexually selected characteristics (Brown, Urban & Newman, 1982; Cramp & Simmons, 1984; Marchant & Higgins, 1990; Del Hoyo, Elliot & Sargatal, 1992; Poole & Gill, 1995). The database and accompanying references are available in the electronic appendix.

Species data

Population trend was represented by 1 = extinct; 2 = decreasing; 3 = stable or fluctuating; 4 = increasing (Wetlands International, 2002). The stable and fluctuating classes were pooled because of the small number of fluctuating populations ($n = 8$ populations). Mean population trend for each species was calculated from the trends of all its populations, weighted by the size of each population size. The IUCN Red List category (Mace & Stuart, 1994) of each species was obtained from www.redlist.org.

The IUCN category is a procedure for assessing the relative probability of extinction of species according to the level of their threat. We scored the IUCN category as: 1 = extinct (EX); 2 = critically endangered (CR); 3 = endangered (EN); 4 = vulnerable (VU); 5 = near threatened (NT); 6 = least concern (LC).

For each species, all population sizes reported in WPE were summed to obtain a total world population size. Global extents of occurrence (in km^2) were obtained from Threatened Birds of the World (TBW, BirdLife International, 2004). Both population size and global extent of occurrence were natural log-transformed before analysis.

Stevens's modification of Rapoport's rule states that toward the equator, the mean sizes of species' ranges become smaller (Stevens, 1989) and Gaston & Blackburn (1996) demonstrate that Anseriformes indeed have larger ranges at higher latitudes. In order to control for the effect of latitude on global extent of occurrence, the latitude of each species' breeding range was scored, based on the midpoint of their ranges. We elected to use broad categories instead of a continuous variable due to the coarse scale of our breeding range data. The following scores were used: 1 = polar, north of 60°N or south of 60°S; 2 = temperate, between 60°N and the Tropic of Cancer 23°27″N or between the Tropic of Capricorn 23°27″S and 60°S; 3 = equatorial, between the Tropics of Cancer and of Capricorn. Following Dunn, Whittingham & Pitcher (2001), migratory status was scored using a three-point scale: 1 = sedentary, individuals move < 100 km between breeding and non-breeding areas; 2 = partial migrant, individuals move 100–1000 km between breeding and non-breeding areas; 3 = full migrant, individuals move > 1000 km between breeding and non-breeding areas.

To quantify habitat generalism, eight broad habitat types were identified following Green (1996): forest, marine, lake wetlands, river wetlands, grasslands, arable land, tundra and scrub. Categorical variables which could take a value of 1 = used or 0 = unused were created for each habitat type, and thus the habitat types of each species were recorded. Summing habitats used for each species yielded a habitat score. Habitat generalism was represented on an eight-point scale from 1 = one habitat type used, through 8 = eight habitat types used.

In order to score trophic level, a text description of the foods eaten by each species was prepared. The species list was then randomized and three observers scored these descriptions blindly to species identity, using the following scale: 1 = 81–100% animal matter; 2 = 61–80% animal matter; 3 = 41–60% animal matter; 4 = 21–40% animal matter; 5 = 0–20% animal matter.

Adult male mass (in grams) and adult female mass (in grams) were used to calculate a mean adult mass. Adult mass was natural log transformed before the analyses. Fecundity is the mean clutch size of each species.

We used two *proxies* of sexual selection. Sexual dimorphism was calculated as log(adult male mass) − log(adult female mass). Data on testes mass (in grams) were obtained from Dunn *et al.* (2001). Testes mass acts as a *proxy*

measurement of sperm-competition (post-mating sexual selection). As large animals tend to have larger testicles, male size was controlled in multiple regressions against population trend using body mass as a predictor variable.

We used dummy variables to score whether or not the following processes threatened each species: habitat loss/destruction; hunting; pollution; human disturbance; accidental human-induced mortality (Todd, 1996). Summing across these variables produced a score between 0 and 5 for total number of different threat processes.

To assess the degree of human impact on each species, a list was made of countries in each species' global range (range states). For each country we collected the following information: area (in km^2), human population in both 1980 and 1990 (United Nations Population Division, 2004). We also collected data on annual water consumption/capita in 1990 as a *proxy* for pressures on wetlands (Gleick, 1998), and the area of agricultural land in 1980 and 1990, to allow the change in area of agricultural land to be measured over that time period by calculating the difference between the area of agricultural land in 1990 and in 1980. We believe the latter measure represents the degree to which wetlands have been lost to farmland (Food and Agriculture Organisation of the United Nations, 2005). Where possible measures of human impact were obtained for 1990, as this leaves a 10-year lag before the estimation of population trends.

Mean human population density (HPD, people $\times$ km^{-2}) in 1990, per capita water consumption in 1990, and area of agricultural land in 1980 and 1990 across all countries in each species' range was calculated, weighted by area of country. This procedure assumes that countries form a part of a species' range proportional to their area. HPD in 1990, water consumption per capita in 1990, area of agricultural land in 1980 and area of agricultural land in 1990 were log transformed before analysis.

Phylogenetic comparative analyses

We used bivariate and multiple least squares linear regression through the origin of phylogenetically independent contrasts (Felsenstein, 1985; Garland, Harvey & Ives, 1992). For most biological traits it is necessary to control for the effects of shared evolutionary history, since data from closely related species cannot be considered to be independent (Freckleton, Harvey & Pagel, 2002; Blomberg, Garland & Ives, 2003). This is as a result of evolutionary change in sister taxa of traits at a rate proportional to time as divergence (branch length) under a Brownian motion model of evolution (Harvey & Pagel, 1991). CAIC (Purvis & Rambaut, 1995) was used to estimate phylogenetically independent contrasts. We used R 2.1.0 (Ihaka & Gentleman, 1996) for statistical analyses.

Our phylogenetic hypothesis was based on a wildfowl supertree (Figuerola & Green, 2000). We set all branch lengths to equal lengths, as no information on branch lengths was available. The phylogenetic tree was pruned to remove taxa not recognized by Monroe & Sibley (1993). Three species of screamers (Anhimidae) were added to the

base of the phylogeny following Livezey (1986). Thus, there are a total of 154 species in our phylogeny.

We ensured heterogeneity of variance in the contrasts generated by CAIC before further analysis, as recommended by Garland *et al.* (1992). We plotted the contrasts in the explanatory variable against the standard deviation of the contrasts. We also tested for significant correlation between the contrasts and their standard deviations as recommended by the CAIC manual, but none were significant.

Multiple regression model

Following bivariate analyses of phylogenetically independent contrasts, a saturated multiple regression model of population trend (response variable) was constructed using all significant ($P < 0.05$) and near-significant ($P < 0.1$) explanatory variables.

A minimum adequate model (MAM) was found by successive removal of the least significant term from the multiple regression model until in the MAM all terms were significant. We were unable to use the Akaike information criterion (AIC) to distinguish between competing models since degrees of freedom were different between models due to missing data (Burnham & Anderson, 2002). We also tested first-order interactions, but since none were significant, these were not included in the final models.

At each stage of modelling CAIC was used to recalculate contrasts in order for sample size to be as high as possible. This is necessary since, when calculating multiple contrasts, a species can only be included in the analysis if data are present for all required variables. Missing data cause sample size to decrease rapidly as more variables are included in the analysis.

Finally, to test whether intrinsic factors differentially predispose species to being at risk from extrinsic factors, we tested the significance of interaction terms between all intrinsic and extrinsic terms remaining in the MAM.

Results

Of 458 populations of 161 Anseriform species, population trends were available for 347 populations. Of these, 10 populations (2.88%) were extinct; 133 populations (38.33%) were decreasing; 121 populations (34.87%) were stable or fluctuating and 83 populations (23.92%) were increasing. The frequency of each trend category was significantly different between continents ($\chi^2 = 62.625$, d.f. = 10, $P < 0.001$, Fig. 1). There are proportionally fewer declining Anseriform populations in North America, Europe and Australasia than in south and central America, Africa and Asia. Wildfowl species in more threatened IUCN categories have lower population trend categories ($r = 0.314$, $P < 0.001$, $n = 129$ contrasts, Fig. 2).

Intrinsic factors

Species with larger population size and global extent of occurrence have more secure population trends (Fig. 3,
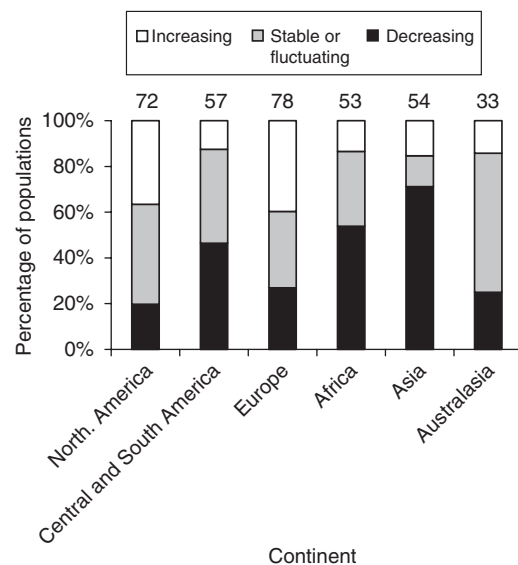

Figure 1 Frequencies of population trends between continents ($n = 347$ populations of wildfowl). The number of populations are above each bar.
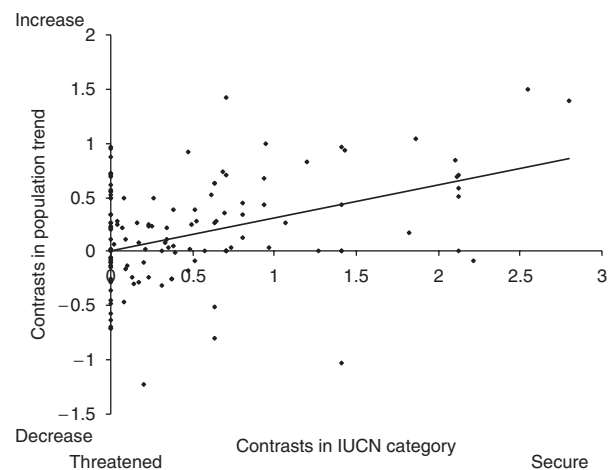

Figure 2 Population trend in wildfowl in relation to International Union for the Conservation of Nature (IUCN) category (least squares linear regression through the origin, $r = 0.134$, $n = 129$ phylogenetically independent contrasts, $P < 0.001$).

population size: $r = 0.438$, $P < 0.001$, $n = 130$ contrasts; extent of occurrence: $r = 0.295$, $P < 0.001$, $n = 121$ contrasts). Neither migratory habit ($r = 0.159$, $P = 0.069$, $n = 130$ contrasts) nor habitat generalism ($r = 0.112$, $P = 0.201$, $n = 130$ contrasts) related to population trends. Furthermore, trophic levels ($r = 0.025$, $P = 0.777$, $n = 129$ contrasts), adult body mass ($r = 0.079$, $P = 0.375$, $n = 126$ contrasts) and fecundity ($r = 0.227$, $P = 0.264$, $n = 107$ contrasts) are not correlated with population trends. However, larger relative testes are correlated with decreasing populations ($r = -0.510$, $P = 0.005$, $n = 37$ contrasts) when body mass of males was corrected for.
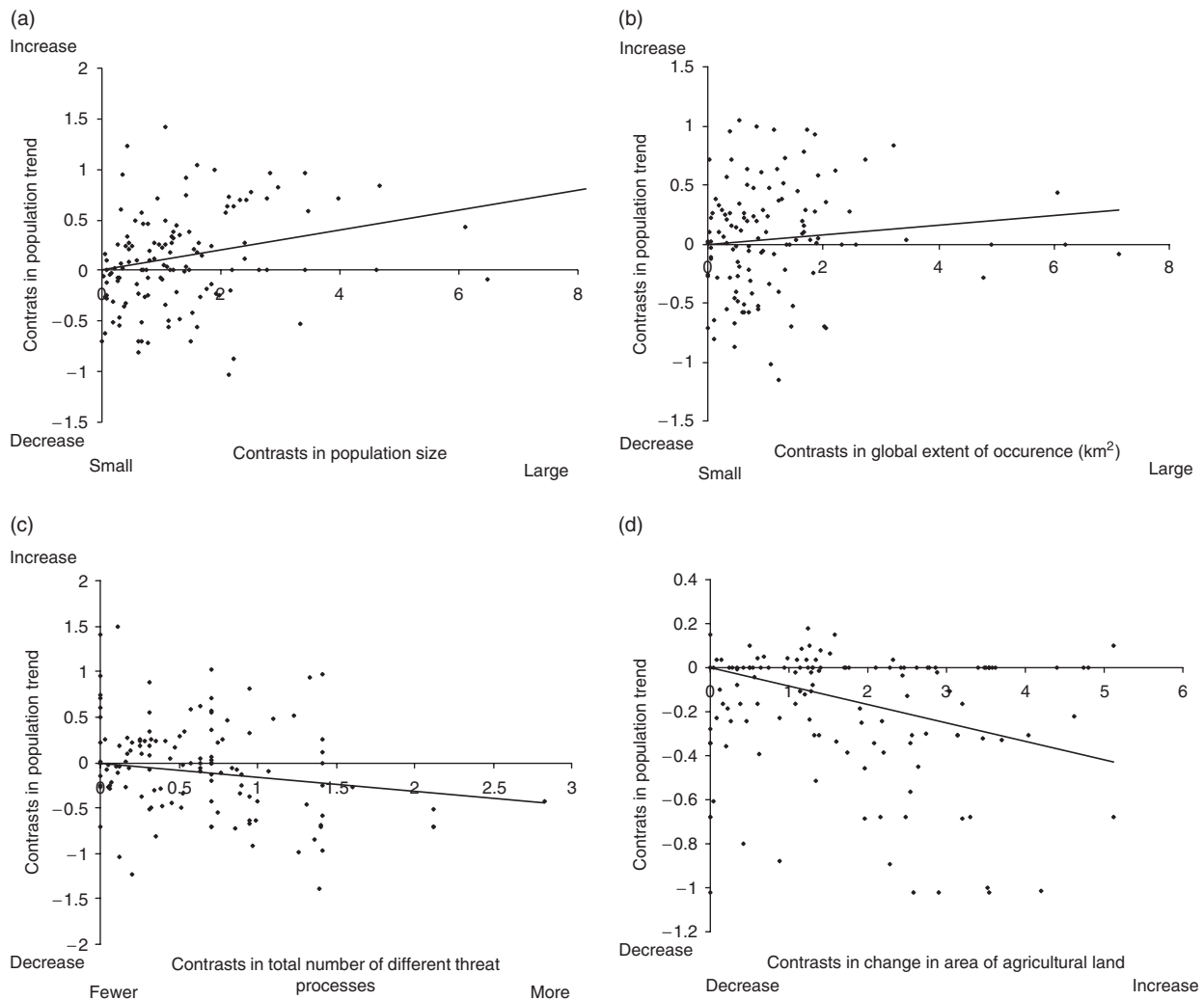
Figure 3 Population trend in wildfowl in relation to (a) population size, (b) global extent of occurrence (c) the number of different threat processes, and (d) change in area of agricultural land. See Table 1 for statistics. Bivariate linear regressions through the origin using phylogenetically independent contrasts.

Extrinsic factors

Neither change in human population density nor per capita water consumption was related to wildfowl population trends (HPD: $r = -0.001$, $P = 0.315$, $n = 129$ contrasts; water consumption: $r = 0.000$, $P = 0.673$, $n = 129$ contrasts). However, increase in the area of agricultural land in a species' range is correlated with decreasing population trend ($r = -0.402$, $P = 0.001$, $n = 129$ contrasts).

A greater number of individual threat processes correlated with decreasing population trend ($r = -0.160$, $P = 0.004$, $n = 129$ contrasts, Fig. 3). In bivariate analyses, habitat loss/destruction ($r = -0.255$, $P = 0.030$, $n = 129$ contrasts), pollution ($r = -0.530$, $P = 0.001$, $n = 129$ contrasts) and invasive species ($r = -0.477$, $P = 0.044$, $n = 129$ contrasts) were significant predictors of a declining population. Hunting did not predict population trend ($r = -0.073$, $P = 0.526$, $n = 129$ contrasts), nor did human disturbance

($r = 0.245$, $P = 0.430$, $n = 129$ contrasts), or accidental mortality ($r = 0.061$, $P = 0.860$, $n = 129$ contrasts).

We used the test statistics from the bivariate analyses, to test whether intrinsic or extrinsic factors predict better population declines. We compared the absolute values of r (Table 1) between bivariate analyses of population trend with intrinsic and extrinsic explanatory variables. The predictive power of intrinsic and extrinsic variables, however, was not different (two-sample t-test, $t_{16} = 0.221$, $P = 0.828$).

Multiple regressions

The minimum adequate model retained population size, global extent of occurrence, number of different threat processes and change in area of agricultural land as explanatory variables (Table 2). Population size, occurrence and change in area of agricultural land remained highly significant in the model, whereas the number of different process

Table 1 Population trend (response variable) in relation to intrinsic and extrinsic threats in wildfowl using phylogenetically independent contrasts (bivariate least squares linear regressions through the origin)

Hypotheses	Explanatory variables	r	No. of contrasts	P
Intrinsic				
Population/range	Population size	0.438	130	<0.001
	Global extent of occurrence	0.295	121	0.001
Ecological	Migration	0.159	130	0.069
	Habitat generalism	0.027	129	0.522
	Trophic level	0.025	129	0.777
	Latitude	−0.153	129	0.257
Life-history	Adult mass	0.079	126	0.375
	Fecundity	0.045	126	0.264
Sexual selection	Testes mass[a]	−0.510	37	0.005
Extrinsic				
Threat processes	Number of different threat processes	−0.160	129	0.004
	Habitat loss/destruction	−0.255	129	0.030
	Hunting	−0.073	129	0.526
	Pollution	−0.530	129	0.001
	Invasive species	−0.477	129	0.044
	Human disturbance	0.245	129	0.430
	Accidental mortality	0.061	129	0.860
Human impact	Change in human population density	−0.001	129	0.315
	Water consumption/capita	0.000	129	0.673
	Change in area of agricultural land	−0.402	129	0.001

[a]Male body mass was also included as an explanatory variable.

Table 2 Minimum adequate model of population trend of wildfowl using phylogenetically independent contrasts

Response variable	Explanatory variables	B	t	P
Population trend	Population size	0.092	2.851	0.0052
	Global extent of occurrence	0.084	2.916	0.0013
	Number of different threat processes	−0.140	−2.112	0.0421
	Change in area of agricultural land	−0.212	−2.259	0.0063

Full model: $r^2 = 0.312$, $F_{4,129} = 8.178$, $P < 0.001$.
Excluded variables: habitat loss, pollution, invasive species.
Slope (B), t-test statistic (t) and probability of t-test statistic (P) are given.

was less so (Table 2). The first-order interactions between intrinsic and extrinsic variables were not significant, so these were eliminated during the process of modelling.

Discussion

Our analyses suggest that both intrinsic and extrinsic factors predict population trends. While the MAM has moderate predictive power ($r^2 = 0.312$) this is quite impressive given the geographically broad scale of study and relatively crude variables represented by scores. The most strongly supported general hypothesis was that a larger population size and range predispose a species to more secure population trend. In the MAM, global extent of occurrence emerged as a stronger predictor of conservation population trend than population size. This contradicts the conclusion of Gaston & Blackburn (1996) who considered that geographic range was less important than the size of the population within that range. Our results suggest that population size and range are closely related, but also that the area of suitable

habitat within a species' range – the area of occupancy – may be a better predictor, since it integrates the two measures.

Green (1996) found that non-migratory wildfowl were in significantly more threatened IUCN categories. He suggests that this result is due to the large number of threatened non-migratory island endemic wildfowl and also argues that the majority of migratory flyways occur at high latitudes in the northern hemisphere where human impacts on wetland habitats are relatively less adverse than at more equatorial latitudes where greater numbers of non-migratory species are found. In our study we found no relationship between migration and population trend. An important difference between our study and Green (1996) is that we carried out the analyses using phylogenetic correction using 130 species for the tests of the migration hypothesis, whereas Green analysed 235 taxa, many of which are non-migratory island sub-species. Thus phylogenetic non-independence of populations (such as in closely related non-migratory *Anas* species that breed on islands) may have biased his results.

Relative testes mass, a *proxy* for the intensity of sperm competition, was significantly correlated with decreasing population trend. This is consistent with the results of Morrow & Pitcher (2003) and Thomas, Lanctot & Szekely (2006), and support the hypothesis that sexual competition may influence population viability in highly sexually selected species. Note however, that due to the small sample sizes, testes mass was not included in the multiple regression models.

An increase in human population density does not directly predict decreasing populations. This may be due to human environmental impacts, such as pollution and hunting, on wetland birds being lesser in more industrialized states. It could also be possible that the most serious habitat modifications took place in the past and that the wildfowl populations observed today have experienced an extinction filter (Balmford, 1996). Interestingly, water consumption per capita does not perform well as a predictor of population trend in Anseriformes. This may because high water use does not necessarily imply high demands on natural wetlands.

The most important extrinsic factors retained in the MAM were the total number of threat processes and the change in area of agricultural land. It is important that both add explanatory power beyond that provided by either population size and geographic range size. This suggests that these external factors may be used to identify regions where wetlands are expected to be increasingly threatened in future. We believe that changes in the area of agricultural land are reflecting destruction or degradation of some types of wetland habitats such as drainage of marshes and shallow lakes which in turn have significant effects on wildfowl populations. That the total number of threat processes is significant, suggests that human threats, which individually do not seriously affect a species, may act synergistically to reduce fitness.

Although in bivariate analyses there was no significant overall difference in the variation in population trend explained by intrinsic and extrinsic factors, our analyses may not have identified other important extrinsic factors driving wildfowl declines. McKinney (2001) argued that the relationship between human population density, anthropogenic habitat modification and animal population decline is complex and may vary geographically and affect different taxonomic groups in different ways. Further research, of extrinsic factors more directly linked to wildfowl populations, such as rates of wetland habitat loss, at multiple spatial scales is needed to address this issue.

Taken together, our results suggest that both intrinsic and extrinsic variables predict the conservation status of wildfowl and that measures of population size and range perform best. Attempts to model conservation status using data on extrinsic threats from human activities are challenging given the complex nature of the interactions and the difficulty of selecting appropriate measures of human impact.

There is great diversity in the proportions of threatened species across bird families. Some families such as Psittacidae and Phasianidae contain substantially more threatened

taxa than may be expected by chance and some such as Picidae contain substantially fewer (Bennett & Owens, 1997). Anatidae and Anhimidae are intermediate families in terms of overall levels of threat.

This study of Anseriformes has allowed us to collate a high-quality dataset to explore in detail the factors affecting extinction risk across a whole global bird order, an approach recommended by Fisher & Owens (2004). The most important intrinsic factors driving declines in wildfowl, population size and range size, have been reported as responsible for declines in other bird groups (Blackburn & Gaston, 2002). However, we believe that the extrinsic factors contributing to declines operate in an idiosyncratic way in different groups. For example, anthropogenic impacts on wetlands are unlikely to affect groups in which forest birds predominate. Further studies exploring how anthropogenic factors operate differently across taxonomic groups, ecological guilds and in different geographical regions would be extremely valuable and have the potential to make great contributions to informing conservation priorities.

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