



Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes

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We examined the effect of body and egg mass, clutch size and incubation period on the occurrence of intraspecific nest parasitism (INP) in Anseriformes and Galliformes, taking into account the phylogenetic relationships of the species concerned. INP has been reported for 46.0% of Anseriformes but only 11.3% of Galliformes, but these rates seem to be underestimates. In both orders INP appears to have multiple origins. Clutch size is significantly larger among INP species and among cavity nesters (all of which are Anseriformes). The length of the incubation period does not differ between INP and non-INP species. After controlling for body mass, we found that the Anseriformes have significantly larger clutches, longer incubation and larger eggs than the Galliformes. We suggest that the large difference in the rate of INP between the two orders is related to the significantly larger clutches of Anseriformes, which increase the period during which clutches are susceptible to parasitism. Furthermore, the larger eggs of the Anseriformes mean that their chicks are more precocial than those of the Galliformes, so that parasitism is less costly in terms of parental care, and less effort is made by nesting females to drive away potential parasites. Lack of coloniality among the Galliformes also contributes to a lower rate of parasitism in this order, because nests are not concentrated in a small space. Lastly, lack of cavity nesting among Galliformes means that competition for nesting sites is lower in this group.

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Intraspecific nest parasitism (INP) in birds has been considered a rare phenomenon in comparison with interspecific parasitism (Payne 1977; MacWhirter 1989), and in 1980 it was reported for only 53 species (Yom-Tov 1980). The growing awareness of the existence of 'alternative' breeding strategies increased the list considerably so that by 1990 it included ca. 200 bird species (MacWhirter 1989; Rohwer & Freeman 1989; Eadie 1991), and presently 236 species (Yom-Tov 2001). A high rate of INP is expected when host nests are available for extended periods of time, because of more opportunities for potential parasites (Andersson 1982; Sayler 1992; Lyon & Everding 1996). Hence, high INP rates are expected in precocial species, because: (1) the majority lay larger clutches than similarly sized altricial species (Ar & Yom-Tov 1978); (2) they start incubating mostly after the last or penultimate egg is laid, leaving the nest without protection for much of the laying period; and (3) parasitic eggs and young among precocial birds require smaller increases in parental care from hosts than in altricial birds (Sorenson 1992). In addition, high INP rates are expected

when nests are crowded into a small space, that is, in colonial species or at high nesting density, and when nest sites are a limiting factor, as they are among nonexcavating cavity nesters (Yom-Tov 1980; Brown & Brown 1988; MacWhirter 1989; Rohwer & Freeman 1989; Lyon & Everding 1996; Beauchamp 1997). However, the rate of INP differs greatly between precocial birds: it is very common among Anseriformes (Eadie et al. 1988; Rohwer & Freeman 1992; Sorenson 1992), but much less so among Galliformes and other precocial orders (Yom-Tov 1980, 2001).

The abundance of INP among precocial birds, particularly in Anseriformes, might also be related to phylogeny. Eadie (1991) examined this for North American Anatidae, and concluded that although INP is a primitive trait in this group, it is not phylogenetically constrained, and the observed variation between species must depend on other, mainly ecological, factors. Beauchamp (1997) has shown that INP in Anseriformes occurs more frequently among colonial-breeding and cavity-nesting species, but failed to find an association between life history and the occurrence of INP. In the conclusion of his study, Beauchamp (1997) recommended that future research should quantify both the occurrence of INP and the various ecological variables that act as determinants.

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Our study is an extension of the work done by [Beauchamp \(1997, 1999\)](#) on INP in Anseriformes. Its primary contribution is the quantitative analysis of magnitude and statistical significance of differences in clutch size, incubation period and egg mass between species having and lacking INP among the two largest orders of precocial birds, namely Anseriformes and Galliformes, while using current research methods that take into account the phylogenetic relationships of the species concerned.

METHODS

Species and their Life History Characters

We gathered data on INP from the ornithological literature, including reviews ([Yom-Tov 1980, 2001](#); [Rohwer & Freeman 1989](#)), books on regional avifaunas ([Ali & Ripley 1968–1974](#); [Cramp & Simmons 1977, 1980](#); [Brown et al. 1982](#); [Urban et al. 1986](#); [Marchant & Higgins 1990, 1993](#); [Maclean 1993](#)), and on particular groups of birds where INP is known to be common ([Johnsgard 1978, 1986, 1988](#)). We considered a species to have INP if one of the above sources described it as such, if it was stated that more than one female laid in one nest but only one female cared for the young (thus excluding communal breeders), or if abnormal clutch sizes were found (larger than twice mean clutch size, [Yom-Tov 1980](#)). The reported cases of INP are underestimates, as can be deduced from the fact that reported rates of INP are higher in areas where most ornithologists work: while the overall rate of INP among Anseriformes is 46% of species, INP was reported in 70% of Anseriformes breeding in the western Palaearctic and North America (U.S.A. and Canada), and in 70% of the species breeding in Australia and New Zealand ([Yom-Tov 2001](#)). These data were complemented with data on nest type (cavity or other) using the above sources and [del Hoyo et al. \(1992, 1994\)](#). Species were defined as cavity nesters even when they sometimes lay in the open. Original references for INP in the various species are provided in [Yom-Tov \(2001\)](#).

INP has been reported in many species, but only a few have been studied extensively regarding its rate. In a recent review, [Power \(1998\)](#) has shown that the rate of INP varies greatly within species. For example, INP rate among acorn woodpeckers, *Melanerpes formicivorus*, ranges from 3.2 ([Joste et al. 1985](#)) to 33.3% ([Mumme et al. 1985](#)) of the broods. Many factors account for this variation, including sampling methods and research effort. INP may also vary on a temporal scale, for example because of temporal variation in the number of active nests available to parasites. Hence, in our analysis, which compares species rather than populations within species, we are unable to account for the intraspecific variance in the rate of INP. For that reason we consider species as either INP or non-INP.

We gathered data on body mass from the above sources and [Dunning \(1993\)](#). When more than one value was given for a parameter, we calculated a mean. Data on clutch size and the length of the incubation period were gathered from [Harrison \(1975\)](#), [Cramp & Simmons \(1977,](#)

[1980\)](#) and [del Hoyo et al. \(1992, 1994\)](#). When a range of clutch sizes was given, we calculated a mean from the common range. We took data on egg length and width from [Schönwetter \(1967–1983\)](#). Egg volume was calculated with the equation $\text{volume} = 0.5 \times \text{length} \times \text{width}^2$, which is a good approximation of both egg volume and egg mass ([van Noordwijk et al. 1981](#)).

Comparisons and Statistics

In this analysis we examined the relationships between mean body mass, egg mass, clutch size and incubation period in the above-mentioned orders. First, we examined the differences between families in each of the four variables, using *t* tests on log-transformed data. In the next step, we removed the effect of body mass prior to testing for differences by using residuals from a regression of each of the three variables on body mass. Last, to control for the effect of phylogeny we used the CAIC program ([Purvis & Rambaut 1995](#)) which implements the independent contrasts method ([Felsenstein 1985](#)). This method identifies comparisons that can safely be regarded as statistically independent based on a given phylogenetic tree. The methods implemented in the CAIC program work best when the variables used are continuous or categorical (preferably dichotomous). Polytomies (nodes with more than two daughter branches) that express ignorance of the true branching structure are treated in CAIC according to [Pagel \(1992\)](#).

A phylogeny for the 34 galliform species is provided by [Kimball et al. \(1999\)](#). We modified this phylogeny by adding data for four additional taxa. Specifically, for each taxon we obtained from a gene bank 1047 bp of the mitochondrial cytochrome b region (accession numbers: Galliformes: AF068193-68190, AF028802-28790, Z48775-48771, AF013763-13761, L08377-8384). Sequences were readily aligned by eye; no deletions or insertions were observed. We constructed a maximum-likelihood tree using the program fastDNAm1 (version 1.0.6, [Felsenstein 1981](#); [Olsen et al. 1994](#)), assuming a transition/transversion ratio of 2.46 and using the global rearrangement option. The ln likelihood for our galliform tree was -13374.7 , and all the branch lengths were significantly larger than zero. A phylogenetic tree for the 146 anseriform species, based on morphological characters ([Livezey 1997](#)), is provided in [Figueroa & Green \(2000\)](#). Tree topologies and branch lengths were coded into the CAIC format for the analyses below.

We examined the relationship between (1) body mass (independent variable) and three other dependent variables (egg mass, clutch size and incubation period) by linear regression, and (2) contrasts of body mass (independent variable) and the contrasts of the other three dependent variables (egg mass, clutch size and incubation period) by linear regression through the origin. We performed these initial steps to examine the effect of body mass on other variables before and after the phylogenetic component was removed. All analyses were performed on log-transformed data.

For our comparisons that controlled for phylogeny, we assigned a value of zero to all species that lack INP or nest

in the open, and a value of one to all species that have INP or nest in a cavity, thus creating categorical variables with only two states. Using the Brunch option in CAIC, we examined all three dependent variables for differences between species having the two states of each categorical variable. The null hypothesis is that evolution in each dependent variable (e.g. egg mass) has not been linked to the character examined (i.e. categorical variable), and thus we should expect half the contrasts in the dependent variable to be positive and half negative, and the mean value of the contrasts to be zero. We tested the null hypothesis using a *t* test on the mean of the contrasts (Purvis & Rambaut 1995). A significant positive mean contrast in any of the variables means that they are varying in the same direction as in the categorical variable (i.e. higher values in species having INP, colonial breeding, or nest in a cavity). A significant negative mean contrast indicates higher values in species that lack INP, breed solitarily, or nest in the open.

To test for correlation between cavity nesting and INP we used two approaches: the concentrated-changes test by Maddison (1990) and a Markov chain model (Pagel 1994). The concentrated-changes test was conducted with the Macintosh program MacClade 3.08a (Maddison & Maddison 1992) and the maximum likelihood approach with the PC program Discrete 4.0 (Pagel 1994, 1997). The concentrated-changes test examines whether changes (losses or gains) in one binary character are more concentrated than expected by chance on those branches selected that are reconstructed to have a particular state in a second binary character. A significant probability would suggest that changes are not randomly distributed and are concentrated within (or outside) the areas distinguished. The program Discrete calculates a ratio between the likelihood of independent evolution of cavity nesting and INP (null hypothesis) and correlated evolution (alternative hypothesis) of these characters. That ratio is tested for statistical significance using a simulated distribution. A significant ratio and higher dependent likelihood value suggest correlated evolution of the two focal characters. In addition, we used the program Discrete to determine the most likely ancestral state of cavity nesting and INP in both bird families.

RESULTS AND DISCUSSION

The Rate and Evolution of INP

Among the 161 and 282 species of Anserimorphae and Gallimorphae, respectively (Monroe & Sibley 1993), INP was reported in no fewer than 74 and 32 species (46.0 and 11.3%), respectively (Yom-Tov 2001). There are not sufficient data on INP for the rest of the species. However, reported rates of INP are higher in areas where most ornithologists work. INP was reported in 70% of the 66 anseriform species breeding in North America and the Western Palearctic (Yom-Tov 2001), and in 37% of the 35 galliform species breeding in these regions. This indicates that the reported rates of INP are underestimates. Since we found phylogenetic and breeding data for only 146 and 38 species of Anseriformes and Galliformes

worldwide, respectively, our further analysis was limited to this sample (Appendix). In our sample, INP occurred among 50.0 and 26.3% of the anseriform and galliform species, respectively. Among the Anseriformes 26.2% were categorized as cavity nesters. Figures 1 and 2 present reconstructions of the evolution of the occurrence of INP in the two orders. The analysis suggests that INP appears to have multiple origins in each clade (Figs 1, 2). However, since in the future some of the species that we categorized as non-INP species might well be found to have this trait, it is conceivable that this conclusion will not hold and INP, at least for the Anseriformes, will be proved to be a common character for the majority of species.

Among birds, cavity nesting is strongly associated with a high rate of INP (Yom-Tov 1980; Andersson 1982; Rohwer & Freeman 1989; Beauchamp 1997), apparently because cavities are a scarce resource for which many females compete. Seven out of the 10 species that branched early in the evolution of the Anseriformes (Fig. 3) are cavity nesters, possibly an indication of the early evolution of this trait in this order. INP was recorded in seven of these species. Twenty more species that evolved later also show cavity nesting and INP. Our analysis suggests that cavity nesting has evolved independently at least three times in the Anseriformes (concentrated-changes test: $P=0.95$; Fig. 3; Maddison 1990), but not at all among the Galliformes. In addition, the likelihood ratio test between cavity nesting and INP was not significant in the Anseriformes ($LR=4.68$, $P=0.83$), indicating no correlated evolution between these traits. Reconstruction of ancestral state using the maximum likelihood approach indicated that in the Anseriformes the ancestral species was not a cavity nester (percentage=16.8%; likelihood= -151.6), but had the INP trait (percentage=87.3%; likelihood= -150.0). The ancestral state of INP in the Galliformes could not be determined with confidence with our data (percentage=53.2%; likelihood= -20.0). These results show that cavity nesting and INP evolved independently in the Anseriformes, and at least INP is a very old trait in this order.

Life History Parameters and Cavity Nesting

After we controlled for phylogeny, among Galliformes the length of incubation period and egg mass were significantly related to body mass, while among Anseriformes only egg mass was significantly related to body mass (Table 1). These significant relationships are in accordance with the findings of Rahn & Ar (1974) and Rahn et al. (1975). After we controlled for both body mass and phylogeny, clutch size in both orders was significantly larger among INP species (Table 2), as found in North American Anatidae (Eadie 1991). Clutch size was also significantly larger among cavity nesters (all of which are Anseriformes). In both orders there was no difference between INP and non-INP species in incubation period (Table 2). Using raw data, incubation period was significantly longer among cavity nesters (as found by Lack 1968), a group where INP is particularly common (see

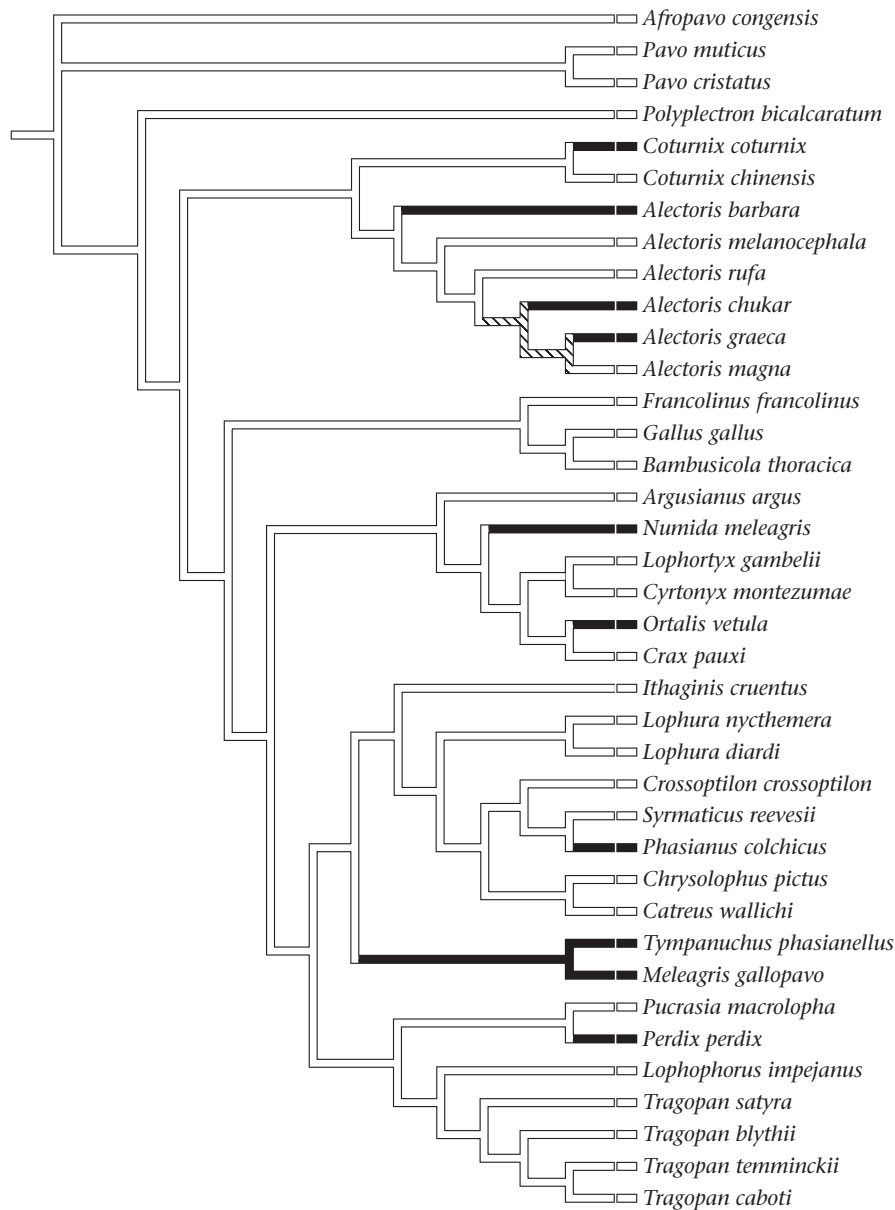


Figure 1. Reconstruction of the evolution of intraspecific nest parasitism (INP) in Galliformes. Branches in black indicate species having INP, branches in white indicate species lacking INP, and hatched branches indicate ambiguity. Branch lengths are not proportional to the real distances between taxa.

above), but this difference disappeared when we controlled for body mass and phylogeny (Table 2). Skutch (1976) argued that extended periods of laying (i.e. larger clutch size) and incubation expose the nest to higher predation pressure. Our results suggest that extended laying periods, but not longer incubation, make nests vulnerable to INP too. No differences were found between colonial and noncolonial species in clutch size, incubation period and egg mass (Table 2). This result may be due to the subjectivity of this variable. In both orders egg mass did not differ between INP and non-INP species; neither was it different in cavity versus open nesters or colonial versus solitary nesters (Table 2).

Beauchamp (1997) found that reproductive effort (indexed by the ratio of clutch mass to female body mass)

differs between INP and non-INP Anseriformes, but emphasized that this variable is confounded by nest location (ground nesters tend to have smaller reproductive effort than cavity nesters). When transitions to INP were examined only in ground nesters, such transitions were equally likely to occur in lineages with small and large reproductive effort. Beauchamp (1999) further examined the effect of coloniality on breeding parameters of pairs of congeners across several orders of birds and found that colonial species do not differ from solitary ones in clutch size, but have larger eggs. However, examining Beauchamp's (1999) predictions by comparing data of 32 pairs (contrasts) of Anseriformes showed that egg mass, when corrected for female body mass, does not differ between colonial and solitary Anseriformes.

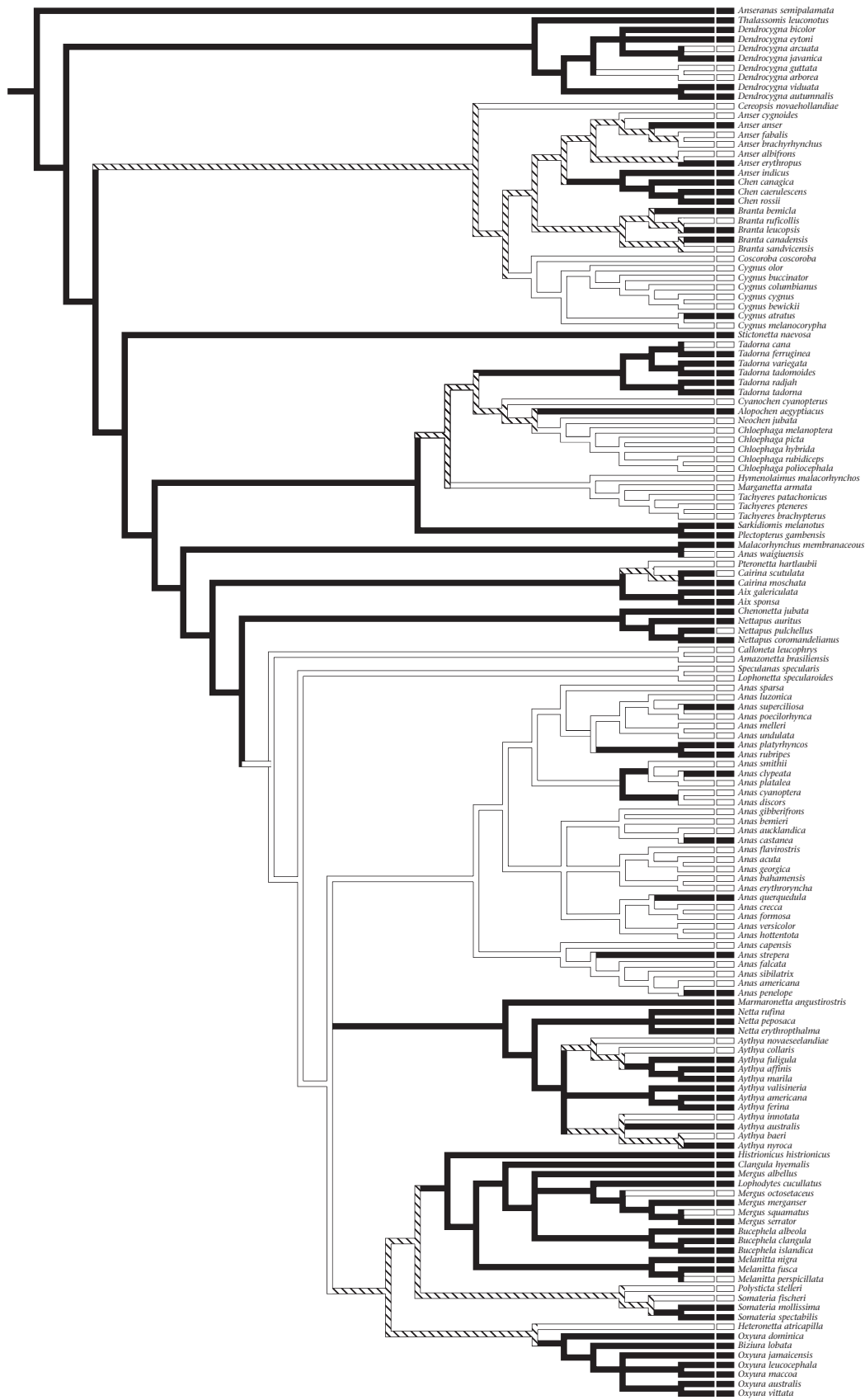


Figure 2. Reconstruction of the evolution of intraspecific nest parasitism (INP) in Anseriformes. Branches in black indicate species having INP, branches in white indicate species lacking INP, and hatched branches indicate ambiguity. Branch lengths are not proportional to the real distances between taxa.

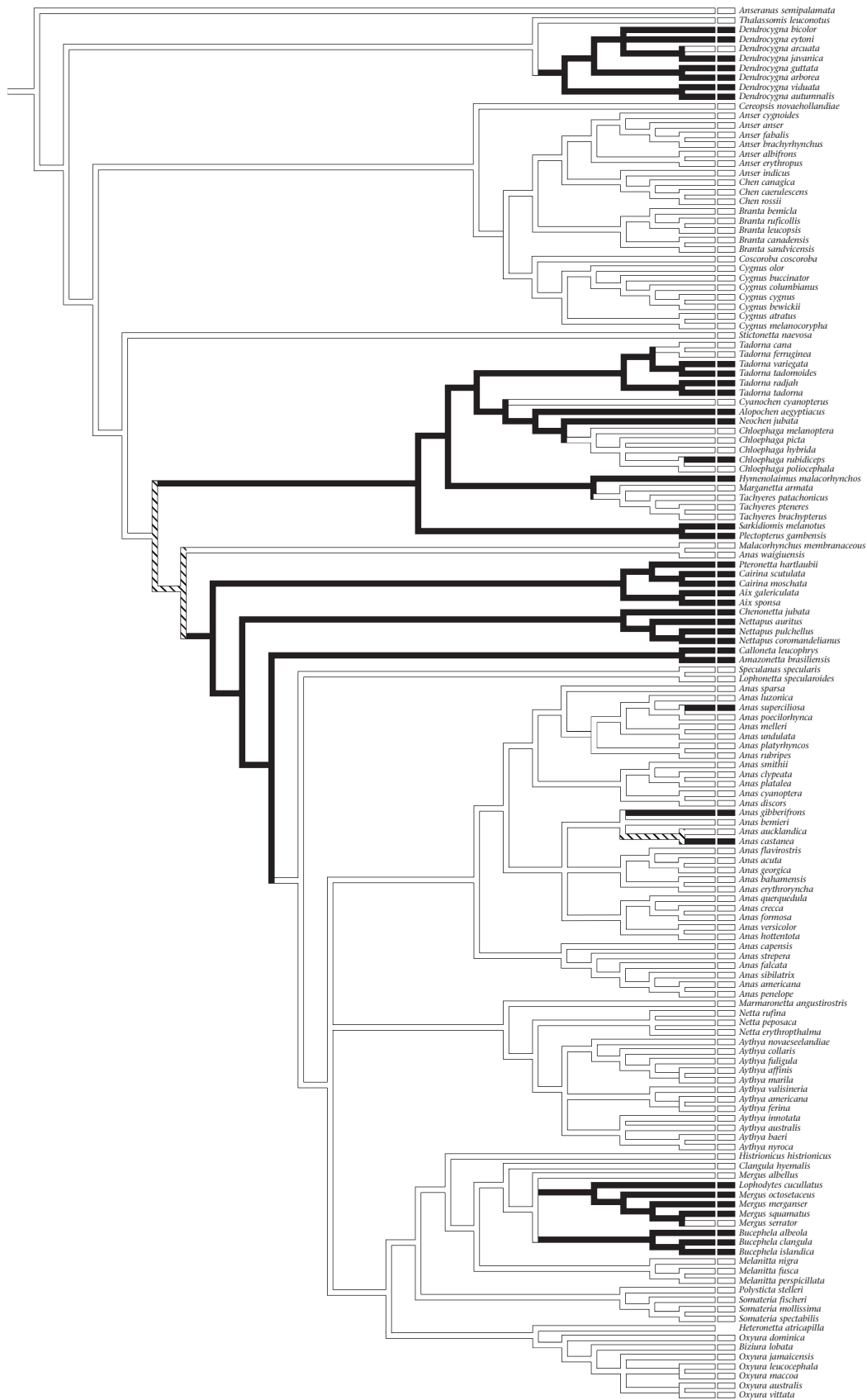


Figure 3. Reconstruction of the evolution of nest site in Anseriformes. Branches in black indicate species nesting in an open nest or a cavity, branches in white indicate species nesting in the open, and hatched branches indicate ambiguity. Branch lengths are not proportional to the real distances between taxa.

Table 1. Regression coefficients of body mass (independent variable) on three reproductive-related dependent variables (clutch size, incubation period, egg mass) in Anseriformes and Galliformes

	Raw data						Contrasts				
	Slope	Intercept	r	F	df	P	Slope	r	F	df	P
Galliformes											
Clutch size	-0.196	1.363	0.31	3.61	1,35	0.066	-0.121	0.19	1.23	1,34	0.274
Incubation period	0.111	1.068	0.71	33.47	1,33	<0.001	0.107	0.71	31.99	1,32	0.009
Egg mass	0.706	-0.537	0.91	153.14	1,32	<0.001	0.655	0.87	100.13	1,31	<0.001
Anseriformes											
Clutch size	-0.164	1.357	0.40	26.85	1,138	<0.001	0.013	0.02	0.08	1,130	0.772
Incubation period	0.060	1.268	0.30	13.06	1,136	<0.001	-0.004	0.01	0.02	1,127	0.877
Egg mass	0.666	-0.224	0.90	558.04	1,134	<0.001	0.438	0.70	120.69	1,126	<0.001

Linear regressions were performed on the raw data (log transformed) and on the independent contrasts (regression through the origin).

Table 2. Differences (*t* tests) in three reproductive-related variables (clutch size, egg mass and incubation period) between (1) species having and lacking intraspecific nest parasitism (INP), (2) single and colonial breeders, and (3) species nesting in a cavity and in the open

	Raw data			Raw data controlled for body mass			Contrasts				Contrasts controlled for body mass			
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>	Mean	<i>t</i>	<i>df</i>	<i>P</i>	Mean	<i>t</i>	<i>df</i>	<i>P</i>
Anseriformes														
INP versus non-INP species														
Clutch size	2.62	141	0.010	2.45	138	0.015	0.026	2.96	34	0.006	0.026	2.63	33	0.013
Incubation period	1.36	136	0.176	1.11	134	0.270	-0.006	1.86	33	0.072	-0.005	1.59	32	0.123
Egg mass	0.60	135	0.548	0.23	132	0.817	-0.019	2.23	33	0.032	-0.013	1.17	31	0.251
Colonial versus solitary species														
Clutch size	0.15	141	0.883	0.13	138	0.896	0.006	0.66	35	0.514	0.009	0.94	33	0.355
Incubation period	4.44	137	<0.001	4.30	135	<0.001	-0.012	1.77	33	0.086	-0.013	1.88	32	0.069
Egg mass	1.47	136	0.143	1.32	133	0.189	-0.011	0.89	32	0.382	-0.018	1.53	32	0.135
Cavity versus open nests														
Clutch size	6.10	141	<0.001	5.44	138	<0.001	0.046	4.94	14	<0.001	0.041	3.41	14	0.004
Incubation period	3.27	136	0.001	3.99	134	<0.001	0.002	0.33	14	0.748	0.002	0.33	14	0.745
Egg mass	2.99	135	0.003	2.93	132	0.004	-0.028	1.79	13	0.097	-0.031	1.62	13	0.130
Galliformes														
INP versus non-INP species														
Clutch size	3.05	36	0.004	3.00	35	0.005	-0.019	2.14	8	0.065	0.020	2.49	8	0.038
Incubation period	0.36	34	0.720	0.86	33	0.932	-0.001	0.29	8	0.779	-0.001	0.56	8	0.589
Egg mass	1.69	33	0.101	3.36	32	0.002	-0.004	0.40	7	0.701	-0.015	2.06	8	0.079

t tests were performed on the raw data (log transformed), on residuals with body mass, on independent contrasts, and on contrasts controlled for body mass (see text for details). A significant positive mean contrast in any of the variables means that they are varying in the same direction as in the categorical variable (i.e. higher values in species having INP, breeding in colonies, or nesting in a hole or a cavity). A significant negative mean contrast indicates higher values in species lacking INP, breeding solitarily, or nesting in the open.

The main reason that among precocial species a large clutch size is associated with INP is that a successful parasite must lay its parasitic eggs over a relatively short period for its young to hatch synchronously with the young of the host. Any eggs laid after the completion of the host clutch will hatch asynchronously, and will be left in the nest after the host hatchlings have departed. Hence, the longer the laying period (because of a larger clutch), the longer the opportunity for a parasite to lay its eggs during the period when they are likely to be incubated to term (Andersson 1982). A long incubation period may also increase the rate of INP, because of the long exposure of the nest to a potential parasite while the incubating parent is away from the nest. However, our

results show that the length of the incubation period did not differ between INP and non-INP species, indicating that this factor has no influence on the rate of INP. This is because if hatching is synchronous, then the likelihood of parasite success does not vary continuously with time since incubation began (although an egg laid a day or two after incubation began may produce a viable chick), but initiation of incubation imposes a threshold.

Do Anseriformes and Galliformes Differ in Life History Parameters?

The large difference in the rate of INP between the two orders (46 and 11.3% for Anseriformes and Galliformes,

Table 3. Mean observed clutch size, incubation length and egg volume, and the same data controlled for body mass, in Anseriformes and Galliformes

	Anseriformes		Galliformes		<i>t</i>	<i>P</i>
	<i>N</i>	Mean±SD	<i>N</i>	Mean±SD		
Raw data						
Clutch size	143	7.65±2.24	38	7.36±3.75	0.62	0.534
Incubation length (days)	139	28.48±5.55	36	24.53±3.51	4.06	<0.001
Egg volume (cm ³)	138	73.21±57.70	35	40.71±33.29	3.20	0.002
Data controlled for body mass						
Clutch size	140	0.02±0.13	37	-0.07±0.25	2.82	0.005
Incubation length (days)	137	0.01±0.07	35	-0.04±0.05	4.18	<0.001
Egg volume (cm ³)	135	0.04±0.11	34	-0.15±0.14	8.43	<0.001

All *t* tests were performed on log-transformed data.

respectively) requires explanation. Hence, we compared female body mass, clutch size, incubation length and egg volume of the two groups by *t* tests carried out on the log-transformed data. These tests are phylogenetically dependent, but there is no way to control here for phylogeny using contrasts because Anseriformes and Galliformes are two separate clades, and there is only a single contrast between them. Our aim in these tests was only to show the observed trends and not to conclude anything about adaptiveness of these traits. We found that after controlling for body mass, the Anseriformes have significantly larger clutches, longer incubation and larger eggs than the Galliformes (Table 3). These differences may account for much of the variation in the rate of INP between the two groups: extended periods of laying expose the nest for longer periods to potential parasites. The relatively larger eggs of the Anseriformes indicate that the hatchling is more developed and independent. Nice (1962) classified the state of maturity of hatchlings of birds on a scale of eight, ranging from complete precocial (P1: birds whose young hatch independent of parents, as in Megapodidae) to complete altricial (birds whose young were totally dependent on their parents, as in Passeriformes). On this scale the Anseriformes were defined as P2 and the Galliformes as P3, the main difference between the two orders is that anseriform chicks find their own food, while those of Galliformes are shown their food by their parents. This means that anseriform parents have to invest less time attending the chicks than galliforms. This is in line with Sorenson's (1992) argument that among precocial birds parasitic young require a smaller increase in parental care from the host than an altricial bird would provide.

In summary, in both orders clutch size was significantly larger among INP species, and among cavity nesters (all of which are Anseriformes). We suggest that the large difference in the rate of INP between the two orders is related to the significantly larger clutches, longer incubation periods and larger eggs of the Anseriformes in comparison with the Galliformes, as well as to the lack of coloniality and cavity nesting among the Galliformes.

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Appendix

The data for the 146 Anseriformes species and 38 Galliformes species used in the comparative analyses

Species	Nest site	INP	Female body mass (g)	Clutch size	Incubation period	Egg volume (cm ³)
Anseriformes						
<i>Aix galericulata</i>	C	Y	512	10.5	29.0	31.8
<i>Aix sponsa</i>	C	Y	635	12.0	30.0	41.6
<i>Alopochen aegyptiacus</i>	C	Y	1650	8.5	29.0	85.0
<i>Amazonetta brasiliensis</i>	C	N	370	7.0	25.0	30.0

Continued

Appendix Continued

Species	Nest site	INP	Female body mass (g)	Clutch size	Incubation period	Egg volume (cm ³)
<i>Anas acuta</i>	O	N	985	8.0	23.0	41.8
<i>Anas americana</i>	O	N	719	8.0	24.0	33.1
<i>Anas aucklandica</i>	O	N	410	5.5	29.5	62.0
<i>Anas bahamensis</i>	O	N	569	8.5	25.0	41.2
<i>Anas bernieri</i>	O	N		6.0		
<i>Anas capensis</i>	O	N	380	8.5	28.0	31.8
<i>Anas castanea</i>	C	Y	590	8.5	26.0	34.9
<i>Anas clypeata</i>	O	Y	590	10.0	22.5	37.6
<i>Anas crecca</i>	O	N	318	9.5	22.0	24.5
<i>Anas cyanoptera</i>	O	N	363	10.5	24.5	29.4
<i>Anas discors</i>	O	N	363	9.5	48.0	25.0
<i>Anas erythroryncha</i>	O	N	566	8.5	26.0	51.8
<i>Anas falcata</i>	O	N	585	7.5	25.0	44.8
<i>Anas flavirostris</i>	O	N	394	6.5	24.0	36.3
<i>Anas formosa</i>	O	N	431	7.5	24.5	29.4
<i>Anas georgica</i>	O	N	535	7.0	26.0	44.8
<i>Anas gibberifrons</i>	C	N	469	7.5	26.0	31.8
<i>Anas hottentota</i>	O	N	250	7.5	24.0	23.4
<i>Anas luzonica</i>	O	N	779	10.0	25.5	45.4
<i>Anas melleri</i>	O	N		7.5	28.5	52.0
<i>Anas penelope</i>	O	Y	724	8.5	24.5	41.8
<i>Anas platalea</i>	O	N	565	6.5	25.0	33.7
<i>Anas platyrhynchos</i>	O	Y	585	11.0	27.5	31.6
<i>Anas poecilorhyncha</i>	O	N	1075	8.0	24.0	48.7
<i>Anas querquedula</i>	O	Y	332	10.0	22.0	25.0
<i>Anas rubripes</i>	O	Y	1100	9.5	27.5	46.4
<i>Anas sibilatrix</i>	O	N	828	6.5	26.0	46.4
<i>Anas smithii</i>	O	N	597	8.5	27.5	35.0
<i>Anas sparsa</i>	O	N	1014	6.0	28.0	59.7
<i>Anas strepera</i>	O	Y	850	10.0	25.0	41.8
<i>Anas superciliosa</i>	C	Y	1025	9.0	29.0	
<i>Anas undulata</i>	O	N	817	8.0	27.5	47.1
<i>Anas versicolor</i>	O	N	373	8.0	25.5	27.6
<i>Anas waigiensis</i>	O	N	469	3.5	28.0	53.6
<i>Anser albifrons</i>	O	N	2460	5.5	25.0	110.8
<i>Anser anser</i>	O	Y	3110	5.0	27.5	143.0
<i>Anser brachyrhynchus</i>	O	N	2520	4.0	26.5	
<i>Anser cygnoides</i>	O	N	3150	5.5	28.0	128.6
<i>Anser erythropus</i>	O	Y	1725	4.5	26.5	91.2
<i>Anser fabalis</i>	O	N	2850	5.0	28.0	127.0
<i>Anser indicus</i>	O	Y	2600	5.0	28.5	124.0
<i>Anseranas semipalmata</i>	O	Y	2071	8.0	24.0	116.6
<i>Aythya affinis</i>	O	Y	790	10.0	24.0	44.8
<i>Aythya americana</i>	O	Y	990	9.0	26.0	60.0
<i>Aythya australis</i>	O	Y	838	10.5	25.0	47.6
<i>Aythya baeri</i>	O	N	680	7.5	27.0	36.8
<i>Aythya collaris</i>	O	N	690	9.0	27.0	
<i>Aythya ferina</i>	O	Y	947	9.0	25.0	60.0
<i>Aythya fuligula</i>	O	Y	1050	9.5	24.0	49.6
<i>Aythya innotata</i>	O	N			27.0	44.0
<i>Aythya marila</i>	O	Y	957	10.5	24.5	49.6
<i>Aythya novaeseelandiae</i>	O	N	610	6.0	28.5	
<i>Aythya nyroca</i>	O	Y	520	9.0	26.0	34.2
<i>Aythya valisneria</i>	O	Y	1190	9.5	24.5	63.8
<i>Biziura lobata</i>	O	Y	1551	2.5	24.0	115.2
<i>Branta bernicla</i>	O	Y	1230	4.0	25.0	85.3
<i>Branta canadensis</i>	O	Y	3314	5.5	27.0	88.8
<i>Branta leucopsis</i>	O	Y	1568	4.0	24.5	93.8
<i>Branta ruficollis</i>	O	N	1094	6.5	24.0	81.8
<i>Branta sandvicensis</i>	O	N	1930	4.0	29.0	173.2
<i>Bucephala albeola</i>	C	Y	334	8.5	30.0	35.6
<i>Bucephala clangula</i>	C	Y	800	9.5	30.0	52.9
<i>Bucephala islandica</i>	C	Y	730	9.5	32.0	62.8

Continued

Appendix Continued

Species	Nest site	INP	Female body mass (g)	Clutch size	Incubation period	Egg volume (cm ³)
<i>Cairina moschata</i>	C	Y	2022	11.5	35.0	62.8
<i>Cairina scutulata</i>	C	N	2487	9.5	34.0	62.8
<i>Callonetta leucophrys</i>	C	N	321	9.0	27.0	29.2
<i>Cereopsis novaehollandiae</i>	O	N	3770	5.0	35.5	118.0
<i>Chen canagica</i>	O	Y	2766	5.0	24.5	102.8
<i>Chen caerulescens</i>	O	Y	2517	4.5	24.0	105.5
<i>Chen rossii</i>	O	Y	1500	4.5	21.5	77.3
<i>Chenonetta jubata</i>	C	Y	800	9.5	28.0	47.6
<i>Chloephaga hybrida</i>	O	N	2041	5.0	30.0	102.5
<i>Chloephaga melanoptera</i>	O	N	3185	7.5	30.0	
<i>Chloephaga picta</i>	O	N	2960	6.5	30.0	92.5
<i>Chloephaga poliocephala</i>	O	N	2200	5.0	30.0	87.5
<i>Chloephaga rubidiceps</i>	C	N	2000	6.5	30.0	74.9
<i>Clangula hyemalis</i>	O	Y	814	7.5	25.0	39.0
<i>Coscoroba coscoroba</i>	O	N	3800	5.5	35.0	180.6
<i>Cyanochen cyanopterus</i>	O	N	1520	5.5	32.0	87.5
<i>Cygnus atratus</i>	O	Y	5100	5.5	41.5	242.9
<i>Cygnus bewickii</i>	O	N	5000	4.0	30.0	231.2
<i>Cygnus buccinator</i>	O	N	10 300	6.0	35.0	340.8
<i>Cygnus columbianus</i>	O	N	6200	4.0	29.5	293.1
<i>Cygnus cygnus</i>	O	N	8100	4.5	35.0	301.1
<i>Cygnus melanocorypha</i>	O	N	4000	6.0	36.0	221.8
<i>Cygnus olor</i>	O	N	9670	6.0	35.5	323.4
<i>Dendrocygna arborea</i>	C	N	1150	9.0	30.0	44.0
<i>Dendrocygna arcuata</i>	O	N	732	10.5	29.0	31.2
<i>Dendrocygna autumnalis</i>	C	Y	849	14.0	28.5	38.0
<i>Dendrocygna bicolor</i>	C	Y	690	10.0	26.0	38.3
<i>Dendrocygna eytoni</i>	C	Y	792	11.0	29.0	32.9
<i>Dendrocygna guttata</i>	C	N	800	11.0	29.5	37.5
<i>Dendrocygna javanica</i>	C	Y	525	9.5	28.0	33.9
<i>Dendrocygna viduata</i>	C	Y	662	8.5	72.0	32.2
<i>Heteronetta atricapilla</i>	Parasite	N	565		21.0	57.1
<i>Histrionicus histrionicus</i>	O	Y	558	6.0	28.5	39.0
<i>Hymenolaimus malacorhynchus</i>	C	N	750	5.5	31.5	65.8
<i>Lophodytes cucullatus</i>	C	Y	540	10.0	32.5	57.4
<i>Lophonetta specularoides</i>	O	N	1000	6.5	30.0	66.7
<i>Malacorhynchus membranaceus</i>	O	Y	344	7.0	27.0	31.8
<i>Marganetta armata</i>	O	N	327	3.5	43.5	51.3
<i>Marmaronetta angustirostris</i>	O	Y	400	10.5	25.0	23.6
<i>Melanitta fusca</i>	O	Y	1200	8.0	27.5	82.9
<i>Melanitta nigra</i>	O	Y	800	7.0	27.5	66.8
<i>Melanitta perspicillata</i>	O	N	900	6.0	27.5	94.1
<i>Mergus albellus</i>	O	Y	568	8.0	28.0	37.5
<i>Mergus merganser</i>	C	Y	1232	10.0	33.5	69.8
<i>Mergus octosetaceus</i>	C	N				66.8
<i>Mergus serrator</i>	O	Y	908	9.0	32.0	63.8
<i>Mergus squamatus</i>	C	N		10.0		
<i>Neochen jubata</i>	C	N	1250	8.0	30.0	58.1
<i>Netta erythrophthalma</i>	O	Y	766	10.0	26.0	52.3
<i>Netta peposaca</i>	O	Y	1004	10.0	28.0	49.4
<i>Netta rufina</i>	O	Y	967	9.0	27.0	51.2
<i>Nettapus auritus</i>	C	Y	260	9.0	23.5	23.4
<i>Nettapus coromandelianus</i>	C	Y	380	11.0		28.8
<i>Nettapus pulchellus</i>	C	N	304	10.0		22.5
<i>Oxyura australis</i>	O	Y	852	5.5	27.0	76.0
<i>Oxyura dominica</i>	O	Y	339	5.0	28.0	45.4
<i>Oxyura jamaicensis</i>	O	Y	500	8.0	25.5	
<i>Oxyura leucocephala</i>	O	Y	593	8.5	24.5	82.5
<i>Oxyura maccoa</i>	O	Y	677	6.0	26.0	85.0
<i>Oxyura vittata</i>	O	Y	560	4.0		71.8
<i>Plectropterus gambensis</i>	C	Y	4700	10.0	31.5	114.5
<i>Polysticta stelleri</i>	O	N	860	7.5		49.6
<i>Pteronetta hartlaubii</i>	C	N	870	9.0	31.0	48.5

Continued

Appendix Continued

Species	Nest site	INP	Female body mass (g)	Clutch size	Incubation period	Egg volume (cm ³)
<i>Sarkidiornis melantos</i>	C	Y	1777	13.0	29.0	57.3
<i>Somateria fischeri</i>	O	N	1630	4.0	24.0	64.8
<i>Somateria mollissima</i>	O	Y	1915	5.0	26.0	96.3
<i>Somateria spectabilis</i>	O	Y	1750	4.5	23.0	59.2
<i>Speculanas specularis</i>	O	N	1567	5.0	30.0	62.0
<i>Stictonetta naevosa</i>	O	Y	842	7.0	28.5	69.6
<i>Tachyeres brachypterus</i>	O	N	3400	7.5	34.0	133.2
<i>Tachyeres patachonicus</i>	O	N	2636	7.0	35.0	102.8
<i>Tachyeres pteneres</i>	O	N	4111	6.5	35.0	128.6
<i>Tadorna cana</i>	O	N	1417	10.0	30.0	87.5
<i>Tadorna ferruginea</i>	O	Y	1100	8.5	28.5	71.9
<i>Tadorna radjah</i>	C	Y	839	9.0	30.0	52.9
<i>Tadorna tadorna</i>	C	Y	1043	9.0	30.0	71.8
<i>Tadorna tadornoides</i>	C	Y	1291	9.0	31.5	81.6
<i>Tadorna variegata</i>	C	Y	1300	9.0	32.5	71.8
<i>Thalassornis leucotis</i>	O	Y	695	7.0	32.5	78.3
Galliformes						
<i>Afropavo congensis</i>	O	N	1145	2.5	27.5	65.2
<i>Alectoris barbara</i>	O	Y	376	11.3	25.0	20.3
<i>Alectoris chukar</i>	O	Y	565	9.5	23.5	20.2
<i>Alectoris graeca</i>	O	Y	530	11.0	25.0	20.2
<i>Alectoris magna</i>	O	N	529	12.3	23.0	18.5
<i>Alectoris melanocephala</i>	O	N	522	6.5		
<i>Alectoris rufa</i>	O	N	453	12.0	23.5	20.0
<i>Argusianus argus</i>	O	N	1645	2.0	24.5	67.3
<i>Bambusicola thoracica</i>	O	N	276	5.0	17.5	15.8
<i>Catreus wallichii</i>	O	N	1130	9.5	26.0	64.9
<i>Chrysolophus pictus</i>	O	N	625	8.5	22.0	25.4
<i>Coturnix chinensis</i>	O	N	38	5.5	17.0	4.4
<i>Coturnix coturnix</i>	O	Y	105	10.5	18.5	8.0
<i>Crax pauxi</i>	O	N	2650	2.0	34.0	176.0
<i>Crossoptilon crossoptilon</i>	O	N	1725	9.0	24.0	52.9
<i>Cyrtonyx montezumae</i>	O	N	176	11.1	25.5	9.2
<i>Francolinus francolinus</i>	O	N	424	9.5	19.5	22.6
<i>Gallus gallus</i>	O	N	768	5.5	19.0	26.8
<i>Ithaginis cruentus</i>	O	N	515	4.5	27.5	26.1
<i>Lophophorus impejanus</i>	O	N	1975	4.0	27.0	64.0
<i>Lophortyx gambelii</i>	O	N	156	13.0	23.0	9.1
<i>Lophura diardi</i>	O	N	853	6.0	24.5	34.7
<i>Lophura nycthemera</i>	O	N	1225	6.9	25.5	38.8
<i>Meleagris gallopavo</i>	O	Y	4000	11.5	28.0	35.4
<i>Numida meleagris</i>	O	Y	1492	9.0	26.0	38.0
<i>Ortalis vetula</i>	O	Y	574	3.0	25.0	
<i>Pavo cristatus</i>	O	N	3375	4.5	29.0	94.6
<i>Pavo muticus</i>	O	N		4.5	27.0	104.8
<i>Perdix perdix</i>	O	Y	380	16.0	24.0	13.6
<i>Phasianus colchicus</i>	O	Y	999	11.5	22.0	29.7
<i>Polyplectron bicalcaratum</i>	O	N	480	2.0	21.0	33.8
<i>Pucrasia macrolopha</i>	O	N	1033	6.0	26.5	35.9
<i>Syrnaticus reevesii</i>	O	N	949	7.5	24.5	31.5
<i>Tragopan blythii</i>	O	N	1250	4.0	29.0	56.6
<i>Tragopan caboti</i>	O	N	900	4.0		40.0
<i>Tragopan satyra</i>	O	N	1100	2.0	28.0	57.3
<i>Tragopan temminckii</i>	O	N	964	4.0	27.0	43.2
<i>Tympanuchus phasianellus</i>	O	Y	815	12.0	23.5	

Nest site: C=cavity; O=open nesting; INP (intraspecific nest parasitism): Y=recorded; N=not recorded. Sources of the data are given in the Methods.