

COMPARATIVE ANALYSIS OF TIME SPENT GROOMING BY BIRDS IN RELATION TO PARASITE LOAD

by

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(With 3 Figures)
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Summary

Although grooming and other kinds of maintenance activity are important components of the behavioural repertoire of terrestrial vertebrates, comparative studies of the proportion of time budgets devoted to maintenance are lacking. Data were collated on the proportion of their time-budgets devoted to maintenance behaviour by 62 different bird species. On average, birds spend 9.2% of the day in maintenance activities, with the major component (92.6%) being grooming. Male birds devoted more time to maintenance than females, except in the case of ducks. Maintenance time does not appear to correlate with morphology, moult, latitude, coloniality or season. However, bird species known to harbour more parasitic louse species spend more time on maintenance than do host species with few lice.

Introduction

Avian maintenance behaviour includes preening, scratching, dusting, sunning, anting, bill wiping, water bathing, smoke bathing, and comfort movements such as stretching (SIMMONS, 1964; DELIUS, 1969). Grooming behaviour, defined as preening and scratching combined (CLAYTON & COTGREAVE, 1994), is the most time-consuming component of maintenance (see below). Grooming serves a variety of functions such as straightening and oiling of feathers and removal of dirt and debris from the body surface (SIMMONS, 1964). It also serves to control harmful ectoparasites (MARSHALL, 1981; CLAYTON, 1991). Birds with impaired preening ability, owing to minor bill deformities (POMEROY, 1962; LEDGER, 1970; CLAY-

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TON, 1989) or experimental manipulation (BROWN, 1972; CLAYTON, 1991), are subject to increased ectoparasite loads that reduce fitness (CLAYTON, 1990; BOOTH *et al.*, 1993).

Despite the importance of grooming and related activities, maintenance is probably the least studied major category of vertebrate behaviour. Many textbooks do not even list "grooming" in their indices (ALCOCK, 1975; BROWN, 1975; TOATES, 1980; BARNETT, 1981; GOULD, 1982; MCFARLAND, 1985). Time devoted to maintenance might constrain time available for foraging and other activities. SWENNEN *et al.* (1989) presented data suggesting that oystercatchers (*Haematopus ostralegus*) do not reduce the amount of time they devote to maintenance behaviour even when time available for foraging (low-water periods) is reduced to one-third of the normal time. Of course, the degree to which maintenance time acts as a constraint would depend on the fraction of overall activity that it represents. Species that devote relatively little time to maintenance are presumably less constrained than those engaging in a lot of daily maintenance. To our knowledge, however, there have been no broad-based comparative analyses of maintenance time in any group of vertebrates. The main goal of this study was to conduct such an analysis using data extracted from published time budget studies on birds.

A second goal of the study was to look for morphological and ecological factors that correlate with the amount of time birds devote to maintenance. We were particularly interested in comparing grooming time to the variables: body size, relative bill length, and parasite load. Interest in the first variable was stimulated by HART *et al.*'s (1992) prediction that small-bodied species spend more time grooming than large-bodied species. The assumption underlying their "body-size principle" is that small-bodied species cannot afford to accumulate as many ectoparasites per unit of body surface, given their larger surface to mass ratio.

Our interest in morphological characters, such as relative bill length, follows from CLAYTON & COTGREAVE's (1994) demonstration that long-billed species of birds spend relatively more grooming time scratching with their feet than do short-billed sister taxa. The assumptions underlying this prediction are 1) that birds with long, unwieldy bills are less efficient at preening than short-billed species, and 2) that birds can compensate for inefficient preening by grooming with their feet. In the current study, we wished to test whether long-billed species also differ

from short-billed species in the amount of overall time they devote to grooming. CLAYTON & COTGREAVE (1994) also noted that leg length may be important for those species which spend a large amount of time scratching, so in the present study we have also considered this.

A measure of parasite load was considered interesting on the basis of the simple prediction that birds with more ectoparasites should spend more time grooming than those with few (HART *et al.*, 1992).

Methods

Data were culled from the literature on what proportion of their daily time budgets birds spend in all forms of maintenance behaviour combined (Table 1). Most workers do not report separate data for different types of maintenance activity, such as scratching, preening, bathing and stretching.

For each study, data were first averaged across the sexes and across sites (within a study) for different observation periods; they were then averaged across observation periods to give an overall mean for the study (observation periods were used as given in the individual studies and varied in their coarseness). Only those data collected during daylight were used and, where a study gave separate values for different times of day, daylight hours were assumed to encompass the period 0700 hrs to 1900 hrs. Where more than one study dealt with the same species, we took the mean value across studies to obtain a final average for the species. For a comparison of grooming time between the sexes, data were included only if both sexes were sampled during the same observation period at the same site.

Estimates of the following variables were also collected for each species: body mass, culmen length, tarsus length and the number of days in the year during which individuals of a species are in moult (British Museum, 1874-1895; CRAMP & SIMMONS 1977-1988; GINN & MELVILLE, 1983; Readers' Digest, 1985; MARCHANT & HIGGINS, 1990; DUNNING, 1992). As a rough measure of parasite load, we also recorded the number of species of chewing lice (Phthiraptera, formerly Mallophaga) found on each bird species, using an unpublished world checklist of known records compiled by R.D. PRICE, a leading expert on this group of insects. More louse species are likely to be known from better-studied species of birds, so we also estimated how well-studied each bird species was. The on-line Science Citation Index was used to count the number of papers published with a species' scientific name in the title, during the five year period 1988-1992, inclusive.

Species were also classed as colonial, semi-colonial or not colonial, using data from the literature, some of which were collated by A.Ø. MOOERS (COTGREAVE & HARVEY, 1994; MOOERS, 1994; MOOERS & MØLLER, submitted). Coloniality data were available for 52 of the 62 species.

Data were analysed using phylogenetic comparative methods (HARVEY & PAGEL, 1991), in particular the paired comparisons of BURT (1989), and the gradual evolution model of PURVIS' (1992) implementation of FELSENSTEIN's (1985) method of analysing independent evolutionary contrasts for continuous variables (see PAGEL, 1992). Copies of the computer programme used are available from Dr. A. PURVIS, Department of Zoology, South Parks Road, Oxford, OX1 3PS, U.K. SIBLEY & AHLQUIST's (1990) phylogeny was used and JOHNSGARD (1961) was consulted for the internal branching structure within the genus *Anas*. The phylogeny is shown in Fig. 1.

The assumptions of the least-squares regression model were best satisfied by the logarithmic transformation of body size, culmen length, tarsus length and the number of published papers but not transforming the proportion of time spent in maintenance behaviour, the duration of moult, or the number of known louse species.

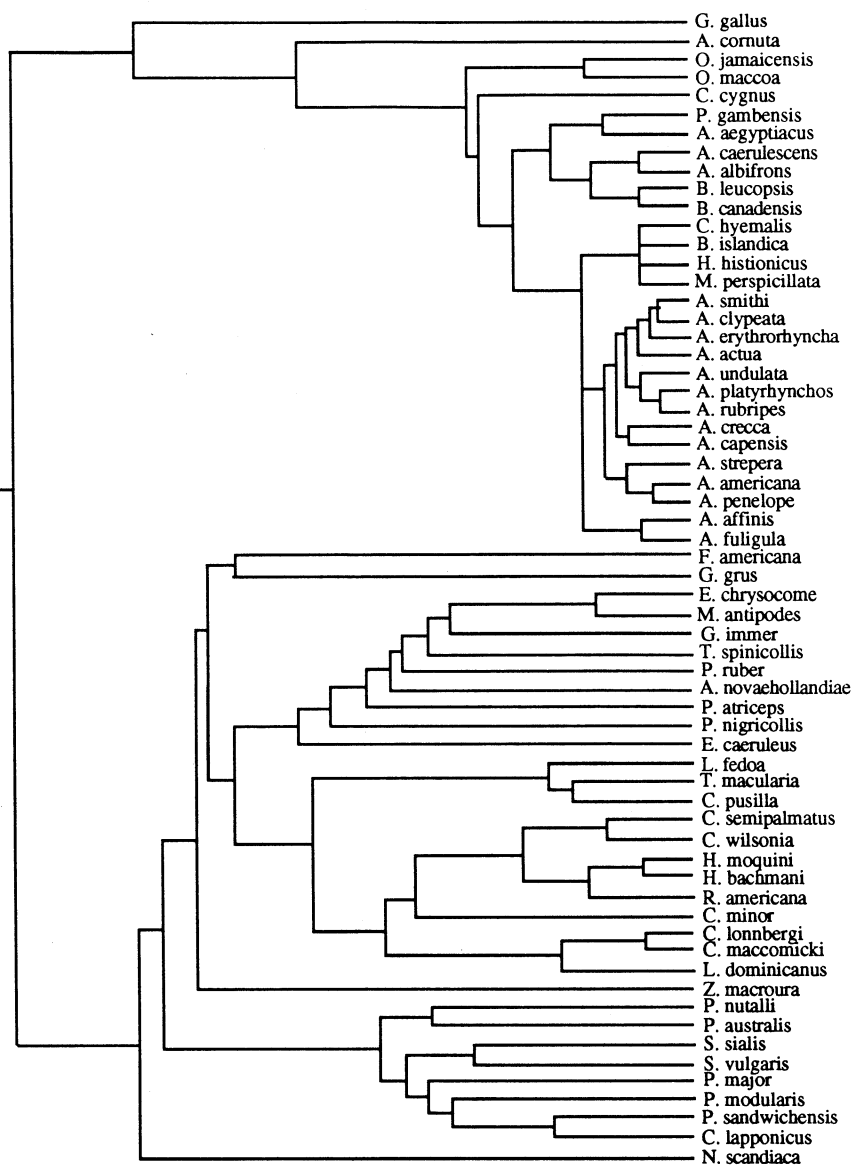


Fig. 1. Phylogeny of the 62 species of birds used in the analyses. The tree follows SIBLEY & AHLQUIST (1990) with JOHNSGARD (1961) consulted for the internal structure of the genus *Anas*. See Table 1 for generic names.

TABLE 1. Proportion of daily time budget devoted to maintenance behaviour by 62 species of birds

Species	Percent of day spent in maintenance behaviour	Winter only	Summer only	Male only	Female only	Reference
Galliformes						
(Chickens etc.)						
<i>Gallus gallus</i>	13.0					DAWKINS, 1989
Anseriformes						
(Ducks, geese, swans)						
<i>Alopochen aegyptiacus</i>	13.0					HALSE, 1985
<i>Anas acuta</i>	10.0	10.3	8.9	13.5	13.7	RUSHFORTH GUINN & BATT, 1985; RAVE & CORDES, 1993; TAMISIER, 1976; MILLER, 1985
<i>Anas americana</i>	8.8					TURNBULL & BALDASSARRE, 1987
<i>Anas capensis</i>	6.9					SKEAD, 1977
<i>Anas clypeata</i>	11.3	7.0	15.6	12.5	13.2	AFTON, 1979; PIROT & PONT, 1987
<i>Anas crecca</i>	7.9	6.9	2.3			QUINLAN, 1984; RAVE & BALDASSARRE, 1989; TAMISIER, 1972; TAMISIER, 1976
<i>Anas erythroryncha</i>	8.1					SKEAD, 1977
<i>Anas penelope</i>	5.2					CAMPREDON, 1981
<i>Anas platyrhynchos</i>	10.9	13.7	6.7	4.7	8.7	ASPLUND, 1981; TITMAN, 1981; PAULUS, 1988; TURNBULL & BALDASSARRE, 1987; JORDE <i>et al.</i> , 1984
<i>Anas rubripes</i>	6.9	7.1	11.7			WOOLEY & OWEN, 1978; HICKEY & TITMAN, 1983
<i>Anas smithi</i>	7.9					SKEAD, 1977
<i>Anas strepera</i>	5.0					PAULUS, 1984
<i>Anas undulata</i>	8.7					SKEAD, 1977
<i>Anhima cornuta</i>	15.6					NARANJO, 1986
<i>Anser albifrons</i>	7.6	8.9	3.8			ELY, 1992
<i>Anser caeruleus</i>	6.4					BURTON & HUDSON, 1978; GIROUX <i>et al.</i> , 1986; FREDERICK & KLAAS, 1982
<i>Aythya affinis</i>	8.1				9.8	10.2 SIEGFRIED, 1978
<i>Aythya fuligula</i>	3.8					PEDRIOLI, 1982
<i>Branta canadensis</i>	11.3				9.4	5.9 ÅSTRÖM, 1993; EBERHARDT <i>et al.</i> , 1989
<i>Branta leucopsis</i>	0.9					EBBINGE <i>et al.</i> , 1975
<i>Bucephala islandica</i>	12.5				12.0	13.0 SAVARD, 1988
<i>Clangula hyemalis</i>	6.0				4.0	8.0 REYNOLDS, 1987
<i>Cygnus cygnus</i>	4.1					BRAZIL, 1981

TABLE 1 continued

<i>Histrionicus histrionicus</i>	16.5		13.9	19.2	INGLIS <i>et al.</i> , 1989
<i>Melanitta perspicillata</i>	3.0				SAVARD & LAMOTHE, 1991
<i>Oxyura jamaicensis</i>	12.2				TOME, 1991
<i>Oxyura maccoa</i>	10.0				SIEGFRIED <i>et al.</i> , 1976
<i>Plectropterus gambensis</i>	13.0				HALSE, 1985
Strigiformes					
(Owls)					
<i>Nyctea scandiaca</i>	3.3				BOXALL & LEIN, 1989
Columbiformes					
(Pigeons & doves)					
<i>Zenaida macroura</i>	23.0				LOSITO <i>et al.</i> , 1990
Gruiformes					
(Cranes, rails, coots)					
<i>Fulica americana</i>	12.4		12.7	12.2	RYAN & DINSMORE, 1979
<i>Grus grus</i>	12.7				ALONSO & ALONSO, 1993
Ciconiiformes					
(Gulls, herons, waders, grebes, raptors etc.)					
<i>Ardea novaehollandiae</i>	9.2	3.0	19.0		LO & FORDHAM, 1986
<i>Catharacta lonnbergi</i>	2.6				PIETZ, 1986
<i>Catharacta maccormicki</i>	3.7				PIETZ, 1986
<i>Charadrius semipalmatus</i>	4.9				MORRIER & McNEIL, 1991
<i>Charadrius wilsonia</i>	1.8				MORRIER & McNEIL, 1991
<i>Chionis minor</i>	13.4		14.1	12.6	BURGER, 1981
<i>Calidris pusilla</i>	2.7		3.5	2.0	ASHKENAZIE & SAFRIEL, 1979
<i>Elanus caeruleus</i>	14.9				TARBON, 1978
<i>Eudypetes chrysocome</i>	0.3				BROOKE, 1985
<i>Gavia immer</i>	25.4				DAUB, 1989; McINTYRE, 1978
<i>Haematopus bachmani</i>	8.1		8.7	7.4	PURDY & MILLER, 1988
<i>Haematopus moquini</i>	14.9				HOCKEY, 1984
<i>Larus dominicanus</i>	7.5		8.8	6.2	MAXSON & BERNSTEIN, 1984
<i>Limosa fedoa</i>	17.2				WISHART & SEALY, 1980
<i>Megadyptes antipodes</i>	11.0				SEDDON & DARBY, 1990
<i>Phalacrocorax atriceps</i>	9.0		9.3	8.7	BERNSTEIN & MAXSON, 1985
<i>Phoenicopterus ruber</i>	23.3				ESPINO-BARROS & BALDASSARE, 1989
<i>Podiceps nigricollis</i>	21.0				ROBERTSON, 1981
<i>Recurvirostra americana</i>	11.6				GIBSON, 1978
<i>Threskiornis spinicollis</i>	6.7				McKILLIGAN, 1979
<i>Tringa macularia</i>	20.6		20.7	17.0	MAXSON & ORING, 1980
Passeriformes					
(Crows, sparrows, starlings, finches etc.)					

TABLE 1 continued

<i>Calcarius lapponicus</i>	2.6			3.4	1.7	CUSTER <i>et al.</i> , 1986
<i>Parus major</i>	4.7					EAST & HOFER, 1986
<i>Passerculus sandwichensis</i>	1.1					WILLIAMS & NAGY, 1984
<i>Petroica australis</i>	3.7					POWLESLAND, 1981
<i>Pica nutalli</i>	4.4	4.9	3.7	2.3	1.4	VERBEEK, 1972
<i>Prunella modularis</i>	5.3					DAVIES & LUNDBERG, 1985
<i>Sialia sialis</i>	6.5					PINKOWSKI, 1979
<i>Sturnus vulgaris</i>	4.7	7.0	3.3			LUNDBERG, 1985

Results

Data were collated on a total of 62 species, representing seven orders (Table 1). Across species, birds spent an average of 9.2 (± 0.7)% of their daylight time budget (about 66 minutes per day) in maintenance behaviour. Individual species values ranged from 0.3% for the rockhopper penguin (*Eudyptes chrysocome*) to 25.4% for the great northern diver (*Gavia immer*). Thirty seven of the 62 species (60%) spent between 5 and 15% of their time budgets in maintenance behaviour. Figure 2 shows the distribution of maintenance time-budgets among the 62 species.

Repeated estimates of maintenance time were used to test repeatability. We plotted repeated estimates against one another (after squareroot arcsin transformation), randomly choosing which data to pair together when there were more than two estimates for a species. This showed a significant repeatability ($N = 11$, $r = 0.67$, $p = 0.02$).

Most studies do not report different types of maintenance behaviour separately but where data were available, grooming comprised an average of about 92.6% of all maintenance behaviour, with about 6.4% of maintenance time spent on bathing and 1% on all other activities. In view of this, we focus on grooming throughout much of this paper.

There are nine species for which separate data were available for the winter and summer months (winter was defined as October to March in the Northern Hemisphere and April to September in the Southern Hemisphere). Of these, six spent more time in maintenance behaviour during the winter and three spent more time during the summer (binomial $p = 0.51$). Seasonal data were therefore pooled in all subsequent analyses.

Using analysis of independent contrasts, there was no relationship between body mass and the proportion of time spent in maintenance

behaviour ($F_{1,56} = 0.43$, $p = 0.52$), nor between the latitude at which a species was studied and the proportion of time spent in maintenance behaviour ($F_{1,56} = 0.52$, $p = 0.48$). Both culmen length and tarsus length were highly correlated with body mass ($F_{1,56} > 37.6$, $p < 0.0005$ in both cases) but after controlling for mass, neither was significantly correlated with the time spent in maintenance behaviour ($F_{1,56} < 0.27$, $p > 0.60$ in both cases). We also looked at the interaction term, by calculating contrasts for the product of tarsus and culmen length. Again this was highly correlated with contrasts in body mass ($F_{1,56} = 80.5$, $p < 0.0005$) and after controlling for this effect, the interaction term was not significantly correlated with time spent in maintenance ($F_{1,56} = 0.18$, $p = 0.67$). Data on the number of days in the year when birds are in moult were available for 37 species. There was no relationship between this variable and the amount of time spent in maintenance behaviour ($F_{1,56} = 0.06$, $p = 0.80$).

The method of analysis of independent contrasts involves the estimation of variables at ancestral nodes on the phylogeny. The logic of doing this with the number of papers published about a species is unclear, so BURT's (1989) test of paired comparisons was used for analyses involving this variable. The number of papers published on a bird species was correlated with the species-richness of lice recorded from the bird ($N = 62$, $r = 0.31$, $p = 0.02$). Taking residuals about this regression gives an

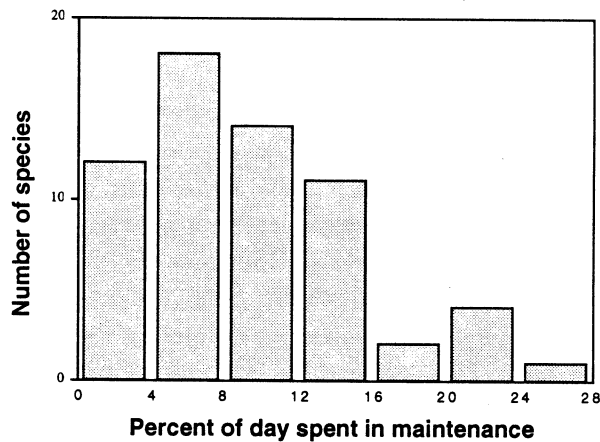


Fig. 2. Distribution of daily maintenance budgets among the 62 bird species in this study. Species which are calculated as spending exactly 4% of their daily budget in maintenance are included in the 4-8% category and so on. The distribution is roughly normal but is truncated at the left.

index of the expected true species-richness of lice from each bird host species. This index was compared with the proportion of time spent in maintenance behaviour using the pairwise comparison method of BURT (1989). It was possible to make a total of 30 comparisons of which one has no variance in maintenance behaviour. Figure 3 shows how, in twenty of the remaining comparisons, the species with the highest index of louse species-richness also spent more time in maintenance behaviour and in nine the trend was reversed (binomial $p = 0.03$). Across the comparisons, species with the higher relative species-richness of lice averaged 17 minutes a day more in maintenance behaviour than the species with lower louse species-richness.

There were 17 species for which separate values of maintenance time could be calculated for males and females. It was not possible to determine how many of these differences were significant, because data are not generally reported for different individual birds, so the variance within each sex could not be calculated. In 10 of the 17 species, males devoted a larger proportion of the day to maintenance behaviour than females and in seven, the reverse was true (binomial $p = 0.62$). However, when species values were averaged to give tribal means, males spent more time on maintenance in nine out of ten tribes (binomial $p = 0.02$). The tribe where

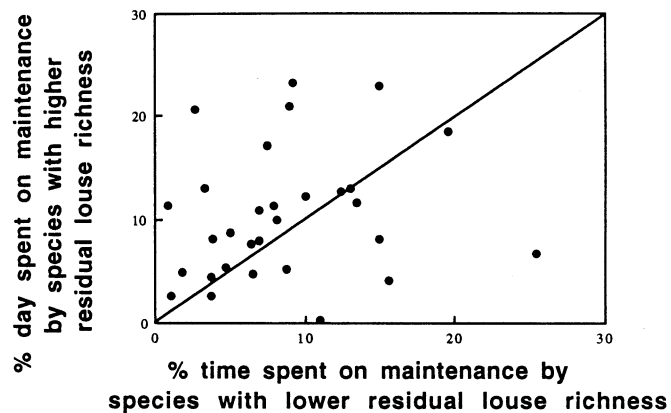


Fig. 3. Sister taxa comparisons of time spent on maintenance relative to louse species richness (controlled for how well-studied the species is). In 20 cases, the species with greater louse richness also spends more time on maintenance and in nine cases, the opposite is true ($p = 0.03$).

females spent more time in maintenance behaviour was the Anatini (ducks).

Data on coloniality and maintenance were analysed using BURT'S (1989) method of pairwise comparisons, since coloniality is scored discretely, not as a continuous variable. We made 17 comparisons, the maximum number possible for which data were available and where there was any variation in coloniality (Table 2). Two of those comparisons are not uniquely defined, e.g. the American avocet *Recurvirostra americana* can be compared to either of the oystercatcher species, *Haematopus* spp. Eleven of the comparisons show the more colonial species

TABLE 2. Sister taxa comparisons of coloniality and time spent on maintenance behaviour

	Non-colonial species	Semi-colonial species	Colonial species	Difference in % time spent in maintenance (more colonial species minus less colonial species)
1	<i>Anser albifrons</i>		<i>Anser caerulescens</i>	-1.2
2		<i>Branta canadensis</i>	<i>Branta leucopsis</i>	-10.4
3	<i>Bucephala islandica</i> or <i>Histrionicus</i> <i>histrionicus</i>	<i>Clangula hyemalis</i>		-6.5 or -10.5
4	<i>Anas clypeata</i>	<i>Anas smithi</i>		-3.4
5	<i>Anas penelope</i>	<i>Anas strepera</i>		-0.2
6		<i>Megadyptes</i> <i>antipodes</i>	<i>Eudyptes chrysocome</i>	-10.7
7	<i>Gavia immer</i>		<i>Threskiornis</i> <i>spenicollis</i>	-18.7
8	<i>Ardea</i> <i>novaehollandiae</i>		<i>Phoenicopterus ruber</i>	+14.1
9	<i>Elanus caeruleus</i>		<i>Podiceps nigricollis</i>	+6.1
10	<i>Calidris pusilla</i>	<i>Tringa macularia</i>		+17.9
11	<i>Haematopus</i> <i>moquini</i> or <i>Haematopus</i> <i>bachmani</i>	<i>Recurvirostra</i> <i>americana</i>		-3.3 or +3.5
12	<i>Chionis minor</i>	<i>Charadrius wilsonia</i>		-12.0
13		<i>Catharacta</i> <i>maccormicki</i>	<i>Larus dominicanus</i>	+3.8
14	<i>Zenaida macroura</i>	<i>Limosa fedoa</i>		-5.8
15	<i>Sialia sialis</i>	<i>Sturnus vulgaris</i>		-1.8
16	<i>Prunella modularis</i>	<i>Passerculus</i> <i>sandwichensis</i>		-4.2
17	<i>Nyctea scandiaca</i>	<i>Pica nutalli</i>		+1.1

The maximum number of comparisons possible with available data were made.

spending less time on maintenance than the less colonial species and five of the comparisons show the opposite trend ($p = 0.21$). The remaining comparison is equivocal, in that the result depends on which oystercatcher species is included (Table 2).

Discussion

Birds average nearly 10% of their daily time budgets in maintenance behaviour. Where it is possible to distinguish among different forms of maintenance behaviour, almost all of the maintenance time of a bird is spent in grooming behaviour. Moreover, some species are known to hold constant the amount of time they spend grooming, even when individuals are constrained with limited time to spend in other activities (SWENNEN *et al.*, 1989). Maintenance activities, especially grooming, clearly form an important component of avian behaviour.

Our results show that birds of different sizes do not appear to spend predictably different amounts of time in maintenance behaviour. Thus we find no support for the prediction that grooming time varies with size (HART, 1992; HART *et al.*, 1992). However, as with all datasets drawn from the literature, negative results should be treated with caution and we do not rule out the hypothesis that time spent grooming may vary with body size in some cases.

Preening (with the bill) and scratching (with the foot) are the components of grooming behaviour in birds and species which have unwieldy bills compensate by spending more of their grooming time scratching (CLAYTON & COTGREAVE, 1994). The present results suggest that this trade-off may even out the total amount of time a bird spends grooming, since neither culmen length nor tarsus length was correlated with the total amount of time birds spend in maintenance behaviour.

Birds which have more continuous moults do not appear to spend more time grooming, which is somewhat surprising. Data on moulting times are generally poor or ambiguous (GINN & MELVILLE, 1983) and it is possible that if better data were available, they might reveal a pattern. Possible confounding effects are that birds with longer moult durations may have a lower intensity of moult, or that birds with a short intensive moult may hide during the moult and thus be difficult to detect. Grooming may also be independent of ambient conditions since we found no

relationship between maintenance behaviour and either season or latitude.

Birds with species-rich louse communities spent more time grooming and this could be explained in two ways. One is that bird lice are known to be site-specific on the host's body (MARSHALL, 1981; CLAYTON 1991), so that a bird with several species of lice might have to spend time removing parasites from more distinct areas of its anatomy than birds that are host to only one or two louse species. An alternative explanation for the result is that birds may groom more in response to higher parasite intensity (number of individual parasites). This assumes that parasite richness correlates with parasite intensity, which is true for the Peruvian birds studied by CLAYTON *et al.* (1992). Their Appendix 1 shows that average number of lice per individual within a species of bird is significantly correlated with the richness of the louse community found on the bird species ($r_s = 0.27$, $N = 88$, $p = 0.01$). This explanation could not be valid if the absence of one louse species allowed others to move into its niche, *i.e.* that the presence of a species competitively excluded others. However, CHOE & KIM (1988) point out that in fact most ectoparasites are so narrowly adapted to their own microhabitats that they do not readily expand their distributions in the absence of potential competitors. Whatever the explanation, the greater time spent grooming by birds with more species of lice represents a potential cost to being colonised by new parasite taxa.

With the exception of the Anatini, male birds in the studies we examined appeared to groom more than female birds. In view of the fact that grooming also correlates with levels of ectoparasitism, it could be that male birds tend to be more heavily parasitised than females. Data are not available to test this hypothesis for the species included in this analyses. Nevertheless, populations of a few species are known where males have higher ectoparasite loads than females (chaffinch, *Fringilla coelebs*, blackbird, *Turdus merula* (ASH, 1960), and seaside sparrow, *Ammodramus maritimus* (POST & ENDERS, 1970)). A larger study, however, failed to find significant sex differences (WHEELER & THRELFALL, 1986). Of the birds collected in Peru by CLAYTON *et al.* (1992), fourteen of the species are represented by at least 12 individuals. Of these, there is one species on which no lice were found, seven in which the males, on average, harboured more lice than the females and six in which the females harboured

