



sets of intrinsic characteristics have been suggested as crucial in determining the net success of food stealing. First, food stealing is often described as a form of aggressive food competition where thieves may use threats or actual physical aggression to force the host to abandon its prey item (e.g. Corkhill 1973; Maxson & Bernstein 1982; Tershy & Breese 1990). According to this aggressive competition perspective, larger birds would be at an advantage over smaller ones (Kushlan 1978; Temeles 1990; Cummins 1995; Willson & Marston 2002). A larger kleptoparasite might increase the probability of hosts yielding their food items, while reducing the probability of the host aggressively defending its prey. Moreover, larger birds have larger eyes and better visual acuity, which may increase the number of kleptoparasitic opportunities they can detect (Fernández-Juricic et al. 2004). Kleptoparasitism should thus be more profitable, and hence have evolved, in lineages characterized by a large body mass, an idea we term the 'brawn' hypothesis.

The second set of skills that might be useful in kleptoparasitic interactions relates to the tactical component of the behaviour. For kleptoparasitism to be profitable, it requires skills to select the appropriate hosts (Bélisle & Giroux 1995; Chavez-Ramirez 1995; Shealer et al. 1997) and to launch an attack from a suitable angle (Dunn 1973; Taylor 1979) or distance (Thompson 1986), using appropriate timing (Hesp & Barnard 1989) and locomotion mode (Burger & Gochfeld 1979). Moreover, it also requires the ability to accurately predict the behaviour of other animals (Krebs & Dawkins 1984) so as to avoid being detected while launching an attack (e.g. Furness 1978; Ens et al. 1990; Spear & Ainley 1993), as well as to anticipate either evasive or aggressive responses and counteractions by the host (Maxson & Bernstein 1982; Amat & Sorriquer 1984). Cognitive abilities allowing the integration and use of more information in decision making might thus increase the probability of kleptoparasitic success. The cognitive skills of animals are thought to be limited by the size of the brain relative to the body (Jerison 1973; Mace et al. 1980). Supporting evidence comes from the findings that the relative size of the brain or of parts of the brain (i.e. neocortex in mammals and telencephalon in birds) are positively correlated to learning speed (Gossette 1968; Riddell & Corl 1977), group size and/or social complexity (Barton 1996; Burish et al. 2004; Shultz & Dunbar 2006), frugivory (Clutton-Brock & Harvey 1980), capture of mobile prey (Garamszegi et al. 2002), innovation frequency (Lefebvre et al. 1997; Reader & Laland 2002) and tool use (Lefebvre et al. 2002; Reader & Laland 2002). Consequently, we predict that kleptoparasites have larger brains than birds that do not rely on this strategy ('brain' hypothesis).

Besides competitive and cognitive skills, the type of prey selected by birds has also been proposed to explain why certain taxa have evolved kleptoparasitism while others have not. In their review, Brockmann & Barnard (1979) noted that almost all kleptoparasitic families were predators including vertebrate prey in their diet. Vertebrate prey are most often large items of high energetic value requiring long handling times, factors that all have been shown to increase the probability and/or profitability of

kleptoparasitic attacks in the field. Birds including vertebrate prey in their diet might therefore encounter profitable kleptoparasitic opportunities more often than birds not feeding on vertebrates, and hence we expect them to have evolved the strategy more frequently ('vertebrate prey' hypothesis). Attacking a host might also bear some similarities to attacking vertebrate prey, preadapting predators to food theft.

In addition to intrinsic attributes of species, some ecological conditions might favour the evolution of food stealing by increasing the probability of encountering, detecting and/or pursuing successful foragers. An ecological condition that might influence the evolution of kleptoparasitism is the social foraging environment of the species. Food stealing has often been reported in large multispecific aggregations of seabirds (Furness 1987). Group feeding might increase the probability of kleptoparasitism because many unsuccessful and successful foragers can then be found in close proximity to each other (Brockmann & Barnard 1979; Amat 1990). The possibility that interspecific food stealing is a consequence of the social environment, which we term the 'group-foraging' hypothesis, may be evaluated by testing whether kleptoparasites tend to join heterospecific foraging groups.

Finally, different types of habitats might offer varying opportunities for kleptoparasitism to be a rewarding strategy. In general, one expects open habitats such as grassland and marine habitats to offer better visibility and hence increase the probability of detecting potential hosts compared with closed habitats such as forests, where hosts might more easily go unnoticed (Paulson 1985). Thus, because of differences in habitat use, bird taxa may encounter kleptoparasitic opportunities at different rates, an idea we term the 'habitat openness' hypothesis.

Our goals in the present paper are four-fold. First, we extensively review the relevant literature looking for field reports of kleptoparasitic behaviour in birds; we then use this information to show that the incidence of food stealing is nonrandomly distributed across avian families. Second, we study the evolutionary history of kleptoparasitism with phylogeny-based methods to assess when and how often the strategy has evolved. The major conclusion of this analysis is that kleptoparasitism is an evolutionarily labile trait that depends on factors other than past history. Consequently, we test the five alternative hypotheses that have been proposed to favour the expression of kleptoparasitism. We use phylogeny-based techniques that allow us to model variation in the incidence of food stealing across lineages as a function of clade traits and environmental variables while accounting for similarity between species due to common ancestry. While it is impossible to unambiguously diagnose the direction of causality by using comparative analyses (Bennett & Owens 2002), we deal with this problem by asking whether early differentiation among avian families in the traits considered as possible precursors of kleptoparasitism has shaped the subsequent evolution of kleptoparasitic strategies within the families. Finally, because we find that kleptoparasitic strategies are expressed more often in large-brained birds, we examine the contribution of potential confounding variables of the relationship

between kleptoparasitism and cognition (juvenile development mode, cerebellum foliation index) and conduct a last analysis at a lower taxonomic level by asking whether kleptoparasitic species have a larger brain than that of their respective hosts.

## METHODS

We defined kleptoparasitism as the stealing of already procured food items (Brockmann & Barnard 1979). We searched for papers on kleptoparasitism in four electronic indexes of scientific publications for the period 1969–2002 (Web of Science, Biosis Preview, Zoological Records and Cisti Source), using keywords such as kleptoparasitism, stealing, piracy, theft, etc. We added these reports to cases listed in Brockmann's & Barnard's (1979) appendix 1. Only papers reporting successful kleptoparasitism cases in which two birds interacted directly were included in the database (the full sequence of appropriation of prey by the kleptoparasite had to be witnessed by the observer). This excluded unsuccessful kleptoparasitic attempts, delayed kleptoparasitism (e.g. pilfering of food caches), and kleptoparasitism between a bird and an animal of another taxonomic group. The question of whether intra- and interspecific kleptoparasitism are two different or similar processes has not been explored directly yet, and thus we have split the cases in inter- versus intraspecific food stealing. In this paper, we concentrate on interspecific reports ( $N = 856$ ; see Supplementary Material, Table S1).

To discard the null hypothesis that kleptoparasitism was randomly distributed across avian clades, we compared the frequency of species within families reported to show food stealing behaviour with that expected from either the total number of species in the family or the research effort devoted to each taxon. For the former, we multiplied the total number of species per family with the average proportion of kleptoparasitic species in the class Aves, 2.0% (197 kleptoparasitic species on a total of 9672; Sibley & Monroe 1990). The frequency of kleptoparasitism expected according to research effort was calculated from the online version of *The Zoological Record*, using the global count of papers published per species between 1978 and 2004. Differences between the distribution of observed and expected frequencies were assessed with the two-sample Kolmogorov–Smirnov test.

The second issue we explored is the importance of evolutionary history in explaining current-day variation in occurrence of food stealing in bird families. We chose to work at the family level because the phylogeny at this level is well supported in birds (Sibley & Ahlquist 1990) and because major diversification in basic life history traits has taken place before or during the establishment of contemporary families (Bennett & Owens 2002). The evolutionary history of food stealing was investigated with two phylogeny-based methods. First, we used parsimony reconstructions (Harvey & Pagel 1991) based on the phylogenetic hypothesis proposed by Sibley & Ahlquist (1990) to map major transitions in the evolution of kleptoparasitism at the family level. A family was considered to have evolved the strategy if it contained at least one species

reported to use kleptoparasitism. Second, we used the phylogeny to estimate the phylogenetic autocorrelation in the proportion of kleptoparasites per family (number of species reported to perform kleptoparasitism/total species in the family) using the spatial autocorrelation statistic Moran's  $I$  (Gittleman & Kot 1990). We estimated Moran's  $I$  with the R package Analysis of Phylogenetics and Evolution (APE), developed by Paradis et al. (2004).

Because the above analyses suggested that food stealing has often evolved within families (see Results), our third goal was to investigate the factors that could explain why some families have evolved kleptoparasitism, whereas others have not. We tested the five hypotheses presented earlier by modelling variation in the incidence of food theft across avian lineages as a function of body size, residual brain size, diet type, mixed-species group foraging and habitat use.

To test the effect of body size on the occurrence of kleptoparasitism, we gathered data on adult body mass for 7288 species, mostly based on information provided in Dunning (1993) and del Hoyo et al. (1992–2005). Repeatability of our body size measures was very high ( $r = 0.99$ ). We used the mean of logged species values (both sexes pooled) to obtain family averages.

Brain mass was available for 1967 species (Mlíkovský 1989a, b, c, 1990; DeVoogd et al. 1993; Székely et al. 1996; Garamszegi et al. 2002; Iwaniuk & Nelson 2002; Iwaniuk 2003). When information was available from different sources, we used mean values. To remove the allometric effect of body size on brain mass (Jerison 1985; Van Schaik & Deaner 2003), we calculated the residuals from a log–log linear regression of total brain mass against body mass on species-level values, and then averaged these residuals within family groups. Our conclusions are robust with respect to the method used to calculate mean residual brain size; we obtained very similar results (not shown) when using residuals from family means of log-transformed body and brain masses (Pagel & Harvey 1989). It has been argued elsewhere that the number of cortical neurons (Roth & Dicke 2005) or the relative size of the nidopallium and mesopallium (Emery 2006) might represent more accurate measures of cognitive abilities. Unfortunately, these measures are only available for a restricted number of species. However, residual brain size correlates closely ( $r^2 = 0.95$ ) with residual number of neurons (Herculano-Houzel et al. 2006; S. Herculano-Houzel, personal communication), and 96% of the variance in the residual size of the mesopallium and nidopallium can be predicted by the residual size of the brain (Nicolakakis et al. 2003). The relative size of the whole brain thus represents a useful proxy for cognitive abilities in birds.

Because motor skills are thought to play an important role in kleptoparasitic behaviour (Brockmann & Barnard 1979), we looked at the contribution of the cerebellum in explaining variation in kleptoparasitic behaviour among bird families. The degree of foliation of the cerebellum is thought to reflect differences in sophistication of motor behaviour in birds and mammals (Butler & Hodos 1996). We thus entered the cerebellar foliation index in a model controlling for differences in body mass (all variables log-transformed prior to analysis). The data used in

this analysis were taken from Table 1 in Iwaniuk et al. (2006). We also examine the partial contribution of juvenile development mode (taken from Bennett & Owens 2002) in explaining variation in the occurrence of kleptoparasitism among bird families because it is a known confounding variable of avian brain size, altricial birds having larger brains as adults than precocial ones (Portmann 1947; Bennett & Harvey 1985).

Information on diet and habitat was taken from Bennett & Owens (2002). For diet type ( $N = 105$  families), we lumped together all categories including vertebrate prey in their diet. This includes 'Higher vertebrates', 'Lower vertebrates' and 'Animals' (a combination of vertebrate and invertebrate prey). We lumped 'Folivore', 'Frugivore', 'Nectar' and 'Invertebrate prey' as diets not including vertebrate prey. On average, vertebrate prey are of large size and energy content compared with invertebrates and vegetable food items, and are thus thought to increase the probability of encountering profitable kleptoparasitism opportunities (Brockmann & Barnard 1979). To characterize habitat use ( $N = 101$  families), we defined five categories, from less to more open habitat types: 'Forest', 'Woodland', 'Scrub and Land', 'Tundra, Grassland, Marsh and Freshwater' and 'Marine'. As intertidal habitats have been suggested before to favour kleptoparasitism for reasons other than habitat openness (e.g. large aggregations; Furness 1987), we ran an additional analysis excluding the 'Marine' category. We obtained similar results with and without this category, and thus present only results using the full data set. Information on participation in mixed-species foraging groups (coded as whether the family does or does not regularly join heterospecific groups;  $N = 100$ ) was taken from the 'Handbook of the Birds of the World' (del Hoyo et al. 1992–2004). We gathered supplemental information ( $N = 24$  families for diet and  $N = 23$  for group foraging) available from descriptions of families in the 'Firefly Encyclopedia of Birds' (Perrins 2003) after we ascertained that the different sources provided similar information (>90% agreement in both cases).

We modelled the occurrence of kleptoparasitism as a function of the above variables, using phylogenetically informed generalized estimating equations (GEEs), as implemented in R using the APE package (Paradis et al.

2004). Traditional statistical techniques assume that all data points are independent from one another, which is often not true in comparative analyses; closely related taxa have a higher probability of sharing characteristics retained from a common ancestor than taxa that are phylogenetically more distant (Felsenstein 1985). Generalized estimating equation (GEE) analyses control for common ancestry by incorporating the phylogenetic relatedness among taxa as a correlation matrix in the model. In these analyses, phylogenetic degrees of freedom ( $df_p$ ) are calculated from the structure of the tree (for more details, see Paradis & Claude 2002). This method yields results that are very close to independent contrasts in terms of type 1 error rate and power (Paradis & Claude 2002). We did in fact obtain similar results with contrasts, but GEE is more appropriate in our case as it provides typical General Linear Model flexibility in the specification of the distribution of the response variable (binomial, Poisson, etc.) and allows us to accommodate both continuous and categorical variables as predictors. In keeping with our objective of examining whether kleptoparasitism was more likely to have evolved within lineages sharing certain attributes or environmental conditions, we characterized each family by the presence or absence of food stealing species and modelled this response variable with a binomial error structure and a logit link. Our results were robust with respect to the inclusion or exclusion of families coded as kleptoparasitic on the basis of only one record ( $N = 6$ ) and we thus present here only analyses using the full data set.

We started the analyses by examining the effect of each predictor individually, including the total number of species per family (log-transformed) as the main confound in each model. Because species richness is closely correlated with research effort (Pearson's correlation coefficient:  $r = 0.70$ ), its inclusion in the models can be thought of as a control for both speciosity and reporting biases. Then, we conducted a multivariate GEE analysis using significant ( $P < 0.05$ ) predictors only.

Our final goal was to validate the results found at the family level using the finer taxonomic level of species. We conducted paired analyses in which each kleptoparasitic species was compared with its host in terms of brain residual and body size. As both birds were foraging at the same location and were interested in the same food item at the moment of their observation in the field, this finer scale of analysis allows us to better control for ecological factors when explaining why one bird ended up winning the interaction while the other bird lost its prey to the kleptoparasite. We compared the kleptoparasite's and the host's relative brain size and body mass (log-transformed) using paired  $t$  tests. In cases where a kleptoparasite was reported to steal from more than one host species, we averaged residual brain and body size values for the different hosts to include each kleptoparasite only once in the analysis. Because in some species body size may differ between sexes, we used sex-specific body mass for the kleptoparasite and/or host when information on the sex of the individuals involved in the event was available from the report, and species averages when it was not.

**Table 1.** Predictors of interspecific kleptoparasitism in five phylogenetically informed univariate GEE analyses

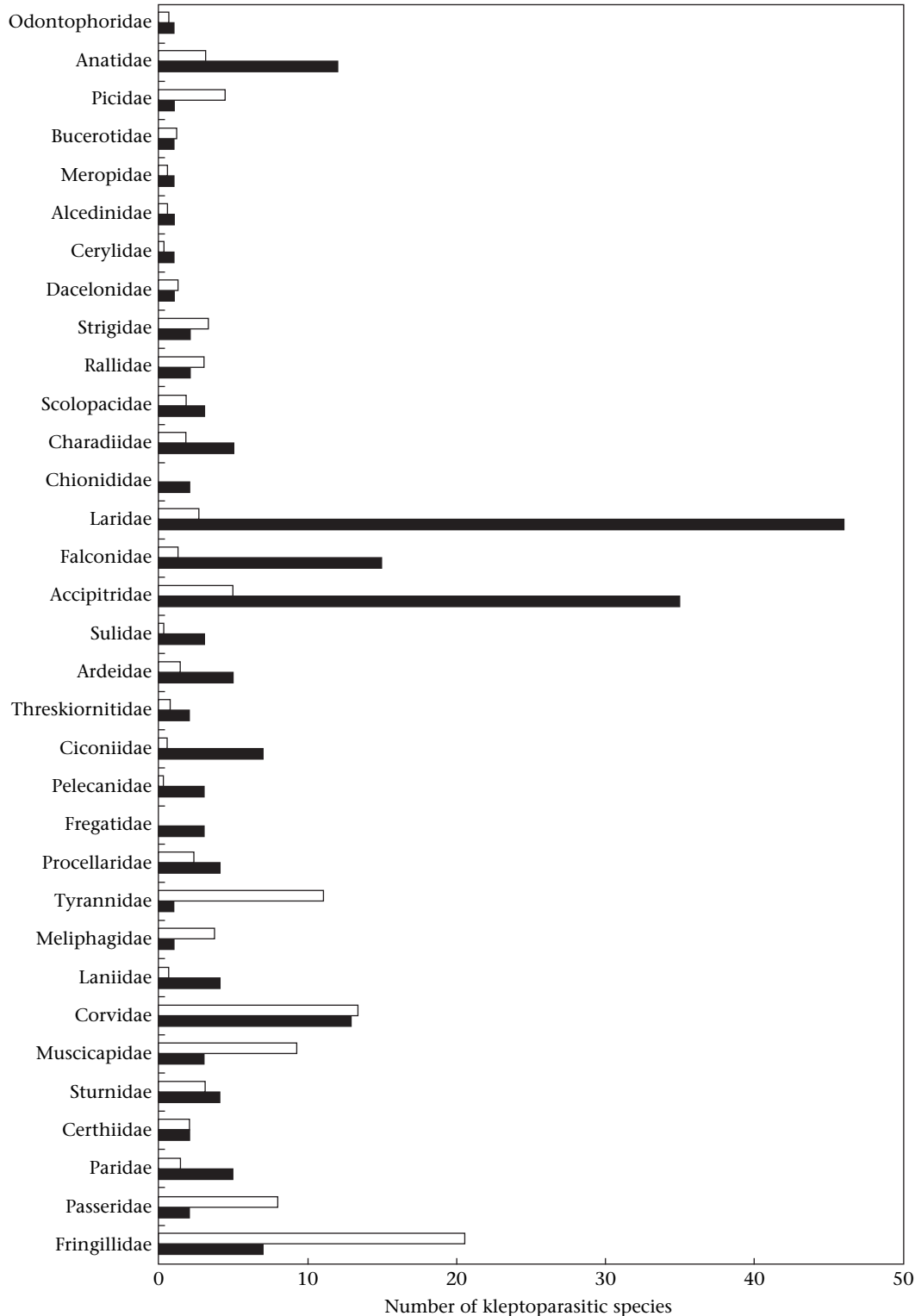
Model	$N$	Estimate	$t$	$P$	$df_p$
1. Nb spp.+body mass	129	0.68	2.05	0.045	68.0
2. Nb spp.+residual brain size	129	0.84	3.51	<0.001	68.0
3. Nb spp.+diet	129	1.87	2.60	0.011	68.0
4. Nb spp.+ multispecific groups	123	0.56	1.19	0.240	65.6
5. Nb spp.+ habitat openness	101	0.77	3.04	0.004	56.1

Each GEEs analysis includes the total number of species per family (log-transformed) as the main confounding variable. The number of phylogenetic degrees of freedom is indicated under  $df_p$ . GEE, generalized estimating equation.

## RESULTS

Our review of the ornithological literature yielded 856 reports of interspecific kleptoparasitism by 197 species from 33 avian families (Fig. 1; see also Supplementary

Material, Table S1). The frequency of kleptoparasitic species was nonrandomly distributed across avian families, either relative to the distribution expected from the total number of species per family (Kolmogorov–Smirnov:  $D = 0.77$ ,  $N = 143$ ,  $P < 0.001$ ; Fig. 1) or that expected



**Figure 1.** Observed (■) and expected (□) number of kleptoparasitic species in the 33 families where kleptoparasitism is present. Expected frequencies are calculated from the total number of species per family. The position of families on the graph reflects their genetic proximity in Sibley & Alquist (1990).

from the research effort devoted to the family (Kolmogorov–Smirnov:  $D = 0.71$ ,  $N = 112$ ,  $P < 0.001$ ).

A parsimony reconstruction revealed that kleptoparasitism has evolved repeatedly in a variety of phylogenetically distant families (see [Supplementary Material](#), Fig. S1). Interestingly, avian families were more dissimilar in the proportion of kleptoparasitic species than would be expected by chance (Moran's  $I$  autocorrelation index  $\pm$  SD:  $-0.0147 \pm 0.0013$ ,  $P < 0.0001$ ), suggesting that the strategy generally evolved within this taxonomic level rather than earlier in the evolutionary history of birds. The conclusion that kleptoparasitism is an evolutionary labile trait is further supported by the finding that within families that have evolved the strategy, only some species engage in stealing food.

The taxonomic distribution of kleptoparasitism among bird families thus cannot be explained solely by differences in speciosity or by phylogenetic autocorrelation. We consequently asked whether families sharing certain attributes or living in some environments have a higher predisposition to evolve kleptoparasitism than families that do not share these attributes or environmental conditions. Having controlled for common ancestry and speciosity, the probability of evolving kleptoparasitic strategies was found to be significantly higher in families characterized by a diet including vertebrate prey, open habitats, enlarged brain residuals and large body masses (Table 1). However, there was no evidence that participation in mixed-species foraging groups was associated with kleptoparasitism (Table 1). A phylogenetically informed GEE model including all of the significant predictors indicated that kleptoparasitism was positively associated with the total number of species per family ( $t = 5.00$ ,  $df_p = 55.1$ ,  $P < 0.001$ ), residual brain size ( $t = 3.69$ ,  $df_p = 55.1$ ,  $P < 0.001$ ), open habitats ( $t = 3.07$ ,  $df_p = 55.1$ ,  $P = 0.004$ ), and diet including vertebrate prey ( $t = 2.07$ ,  $df_p = 55.1$ ,  $P = 0.043$ ), while body mass was not significant in this final model ( $t = -0.71$ ,  $df_p = 5.1$ ,  $P = 0.139$ ).

To verify that the association between kleptoparasitism and residual brain size was not due to the potentially confounding effect of juvenile development mode, we included both predictors in a multivariate phylogenetically informed GEE analysis. Residual brain size remained significantly associated with kleptoparasitic behaviour ( $t = 3.04$ ,  $df_p = 55.8$ ,  $P = 0.004$ ) while controlling for total number of species ( $t = 4.80$ ,  $df_p = 55.8$ ,  $P < 0.001$ ) and juvenile development mode ( $t = 0.06$ ,  $df_p = 55.8$ ,  $P = 0.95$ ).

The importance of residual brain size in explaining variation in kleptoparasitic behaviour in bird families might be interpreted in terms of improved cognitive abilities and/or perception and motor skills in large-brained birds. To examine the latter possibility, we entered cerebellar foliation index in a phylogenetically informed multivariate model controlling for speciosity and body mass. Using this restricted data set ( $N = 37$  families), the cerebellum foliation index was not a significant predictor of kleptoparasitic behaviour in bird families ( $t = -1.09$ ,  $df_p = 23.1$ ,  $P = 0.29$ ).

Finally, we found further support for the finding that kleptoparasitism is associated with cognition rather than to

aggression in a species-level analysis comparing differences in residual brain size and body mass between kleptoparasites and their host(s). Kleptoparasites had a larger residual brain size than their respective hosts (paired  $t$  test:  $t_{138} = 2.13$ ,  $P = 0.035$ ). However, thieves were not heavier than their hosts (paired  $t$  test:  $t_{190} = 0.37$ ,  $P = 0.709$ ).

## DISCUSSION

Kleptoparasitism is a widespread phenomenon in birds and has evolved several times in the evolutionary history of the class. The evolutionary lability of kleptoparasitism may in part come from its opportunistic nature; avian kleptoparasites are capable of obtaining food through a wide variety of feeding techniques in addition to food stealing (Brockmann & Barnard 1979). Thus, food stealing might be a form of flexible foraging that allows predators to survive periods of low food availability. Support for this conclusion comes from the fact that stealing is often reported in the context of food shortages (e.g. Miller & Tilson 1985; Oro 1996). Nevertheless, the predisposition to develop kleptoparasitic behaviours is nonrandomly distributed across avian taxa, and appears to be associated with certain attributes of the taxa. In particular, the possession of a large brain, the use of open habitats and the inclusion of vertebrate prey in the diet appear to have played an important role in favouring the evolution of kleptoparasitic feeding strategies in birds.

In their classic review, Brockmann & Barnard (1979) already noted that almost all kleptoparasitic families were predators including vertebrate prey in their diet. Vertebrate prey have a high energy content, are highly mobile and difficult to locate and/or capture, making kleptoparasitic attempts on this type of items absolutely and relatively more profitable than on other prey types (vegetable matter and invertebrates). Moreover, it is possible that morphological and behavioural adaptations useful for hunting vertebrate prey increase the probability of detecting and successfully exploiting kleptoparasitic opportunities in these taxa. Indeed, locating, pursuing and catching a prey from a mobile host might bear some behavioural similarities with hunting mobile vertebrate prey. In frigatebirds, morphological adaptations allowing great speed and manoeuvrability in flight (see Nelson 1975) may be useful both in surface snatching of fish and in aerial pursuit of hosts. An evolutionary pathway from predation to kleptoparasitism has been proposed for *Argyrodes* spiders that might have evolved stealing of insects from their host's web following missed predation events on web-building spiders (Vollrath 1984).

Our results are also consistent with Barnard's (1984) suggestion that scroungers are often opportunistic foragers with good cognitive capacities. Kleptoparasites had a larger residual brain size than their respective hosts foraging in the same environmental conditions. We also found that kleptoparasitism has evolved more frequently within families with larger brains relative to their body size, even after taking into account the effects of speciosity, diet type and common ancestry. This effect was not confounded by juvenile development mode, a well-known predictor

of residual brain size in birds (Portmann 1947; Bennett & Harvey 1985). The possession of a large brain is thought to confer higher behavioural flexibility and information-processing abilities, which might increase the probability of noticing and exploiting successfully kleptoparasitic opportunities. However, larger brains might also allow for improved perception and motor skills, which might be equally useful in stealing from fleeing hosts. Sophistication of motor behaviour is thought to be reflected in the degree of foliation of the avian cerebellum (Butler & Hodos 1996). We found no evidence that cerebellar foliation index could predict variation in kleptoparasitic behaviour among the 37 families for which data were available. This does not mean that motor skills do not play a role in food stealing, only that the cognitive abilities associated with a large brain are better predictors of kleptoparasitic behaviour than are more specific differences in cerebellar foliation. This conclusion is in any case tentative, as the taxonomic data set for cerebellar foliation is currently much smaller than that of whole brain size.

The precise role of cognition in successful interspecific kleptoparasitic acts has not been extensively studied yet, but some field studies suggest an effect of learning independent of physical maturation and/or social dominance. For example, immature black-headed gulls, *Larus ridibundus*, are less successful kleptoparasites than adults, despite no apparent differences in body dimensions and in the speed and strength of attacks (Hesp & Barnard 1989). Success of immatures increased as they engaged in fewer mistimed attacks, which often led to detection of the attack and evasion by lapwings, *Vanellus vanellus*.

The important finding that kleptoparasitism is associated with brain size can be contrasted with the weak evidence supporting a similar role for contest competition skills. In univariate analyses, kleptoparasitism was positively associated with body mass at the family level, but this effect was lost in the multivariate analysis including other predictors. In the species-level paired analysis, thieves were not found to be significantly larger than the hosts they steal from. Similarly, in a review on kleptoparasitism in seabirds, Furness (1987) found 33 pairs of kleptoparasites where the victim was heavier than the host, and 21 with the opposite pattern, resulting in no significant differences in body mass between kleptoparasites and their hosts. Larger birds might be at an advantage in contexts where they can use threats or actual physical aggression on the host ('aggressive kleptoparasitism' in Giraldeau & Caraco 2000), but not necessarily in cases where the kleptoparasite surprises the host and leaves with the prey before the host can detect or react to the attack ('stealth kleptoparasitism' in Giraldeau & Caraco 2000). Furthermore, acceleration speed might be important in many kleptoparasitic pursuits, and a smaller body then provides a higher power output (Pennycuik 1975). These conflicting effects might explain the weak predictive power of body size in explaining the distribution of kleptoparasitism in birds. However, it is still possible that the use of family and species averages has masked the size differences that might exist between each individual kleptoparasite and its victim, despite our effort at minimizing this possibility by using sex-specific body mass

whenever possible in the paired analysis conducted at the species level.

Habitat openness was positively associated with the presence of kleptoparasitic behaviour among bird families. This result is consistent with the use of covered areas by some birds of prey and mammalian carnivores to reduce kleptoparasitic losses (Fischer 1985; Newton 1986; Packer 1986). Paulson (1985) also noted that 10 out of 22 species foraging primarily in open habitats have been reported to engage in food stealing while none of the 10 woodland species do so. However, neither Paulson (1985) nor this study controlled for the increased probability of researchers to detect kleptoparasitic interactions in open habitats. Further studies controlling for this confounding factor would allow a more definitive conclusion on the role of improved visibility in open habitats on the evolution of avian food stealing.

Participation in mixed-species foraging groups was not a significant predictor of the presence or absence of kleptoparasitism among avian families. The social environment of foragers might still impact on food stealing rates, with kleptoparasitic species engaging in more frequent attacks and/or obtaining higher success when participating in mixed aggregations, but interspecific sociality itself might not lead to the development of food stealing habits in taxa that have low behavioural flexibility. In mixed-species foraging groups, larger-brained species usually rob smaller-brained ones, despite the fact that both species feed simultaneously on the same food items in the same ecological conditions. For example, gulls, *L. ridibundus*, rob earthworms from lapwings, *V. vanellus*, and golden plovers, *Pluvialis apricaria* (Thompson 1986), while drongos, *Dicrurus paradiseus*, steal insects from laughing thrushes, *Garrulax pectoralis* (King & Rappole 2001), but the reverse is not observed.

The finding that avian kleptoparasites may be depicted as large-brained predators not only confirms previous suggestions by Brockmann & Barnard (1979) and Barnard (1984), but also emphasizes the general importance of clade attributes in the evolution of kleptoparasitism. These results do not invalidate the case-by-case importance of other factors such as social dominance or social environment in determining kleptoparasitic success, but suggest that these factors are unlikely to be general explanations for understanding why certain taxa have evolved interspecific kleptoparasitism, whereas others have not. A major implication of our conclusions is the need to give more attention to cognitive processes in the study of heterospecific kleptoparasitic strategies. To date, most studies looking at cognitive abilities related to food stealing and prevention of thievery have examined interactions within species rather than among species. These studies have revealed surprising flexibility in protection behaviours by potential hosts (e.g. food caching corvids, reviewed in Dally et al. 2006) and kleptoparasitic tactics (e.g. ravens act inconspicuously while watching conspecifics caching food, Bugnyar & Kotrschal 2002; pigs follow and displace knowledgeable subordinates, Held et al. 2000; baboons use a conspecific in displacing a competitor from food, Byrne & Whiten 1985). Some avian taxa even appear capable of creating kleptoparasitic opportunities by giving false

alarm calls and stealing items while flock mates are engaged in antipredator vigilance (Munn 1986; Møller 1988). This type of behaviour allows stealing from conspecifics as well as heterospecifics, and might represent just one of the tactical behaviours performed by birds to usurp a desirable food resource. Deceptive acts by primates are often performed in food-related contexts, and are more frequent in species with a large neocortex (Byrne & Corp 2004), drawing an interesting parallel with our findings in birds.

### Acknowledgments

We thank Emmanuel Paradis and Brian McGill for statistical advice. We are also grateful to Vincent Careau and two anonymous reviewers for valuable comments on a previous version of the manuscript. Funding for this work was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to L.L. and NSERC and FQRNT scholarships to J.M.F.

### SUPPLEMENTARY DATA

Supplementary data for this article can be found, in the online version, at [doi:10.1016/j.anbehav.2007.04.031](https://doi.org/10.1016/j.anbehav.2007.04.031).

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