The predation cost of being a male: implications for sex-specific rates of ageing

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Evolutionary theory predicts that the rate of extrinsic (i.e. age- and condition-independent) mortality should affect important life history traits such as the rate of ageing and maximum lifespan. Sex-specific differences in mortality rates due to predation may therefore result in the evolution of important differences in life history traits between males and females. However, quantifying the role of predators as a factor of extrinsic mortality is notoriously difficult in natural populations. We took advantage of the unusual prey caching behaviour of the barn owl *Tyto alba* and the tawny owl *Strix aluco* to estimate the sex ratio of their five most common prey. For all prey species, there was a significant bias in the sex ratio of remains found in nests of both these owls. A survey of literature revealed that sex-biased predation is a common phenomenon. These results demonstrate that predation, a chief source of extrinsic mortality, was strongly sex-biased. This may select for alternate life history strategies between males and females, and account for a male life span being frequently lower than female lifespan in many animal species.

The physiological deterioration of organisms as they age presents an evolutionary paradox: if organisms can function well in youth, why can they not continue to do so in old age. Evolutionary hypotheses propose that aging evolves because of trade-offs with survival and fertility late in life being sacrificed for the sake of early reproduction and survival (the optimality explanation; Williams 1957, Rose 1991, Partridge and Barton 1993), or because of weaker selection against late-acting mutations (mutational explanation; Medawar 1952, Williams 1957, Hamilton 1966). A prediction of these hypotheses is that the rate of ageing should increase and the average lifespan decrease as the rate of mortality resulting from environmental factors (extrinsic mortality) increases (Medawar 1952, Williams 1957, Rose 1991).

Evidence that longer maximum lifespan occurs in organisms that have lower extrinsic mortality rates in the wild comes from the comparison of distantly related taxa. Birds and bats, which evade terrestrial predators by flight, generally have greater potential longevities than similarly sized terrestrial vertebrates (Promislow and Harvey 1990, Austad and Fischer 1991, Brunet-Rossinni and Austad 2004). Similarly, animals with thick shells tend to live longer than animals without armours (Gibbons 1987). Extreme maximum lifespan also occurs in social insects where queens live in colonies that are sheltered and heavily defended against predators (Keller and Genoud 1998). In naked mole-rats, the evolution of sociality in subterranean burrows has been accompanied by a reduction of intrinsic mortality and a lifespan increase (Sherman and Jarvis 2002). However, these wide comparisons have shortcomings and should be considered as consistent with the evolutionary theories of ageing rather than rigorous tests (Rose 1991, Partridge and Barton 1993). Results of selection experiments in the laboratory are also consistent with predictions of evolutionary theories of ageing. Experimental studies on flies have demonstrated a strong effect of extrinsic sources of mortality on the rate of ageing (Reed and Bryant 2000, Stearns et al. 2000).

An alternative possible method to test evolutionary theories of ageing consists in conducting intraspecific studies between classes of individuals exhibiting alternative life histories (Chapuisat and Keller 2002). One such test consists in comparing male and female intrinsic longevity in species where sexes exhibit differences in extrinsic mortality. In many mammals and birds one sex has a longer average lifespan than the other (Allman et al. 1998, Moore and Wilson

2002, Fox et al. 2003, Toïgo and Gaillard 2003), with females usually living longer than males (Promislow 1992, Promislow et al. 1992). However, for the vast majority of species it is unknown whether this difference stems from variations in intrinsic (environment-independent) or extrinsic (environment-induced) mortality. Here we propose to take advantage of the peculiar prey caching behaviour of owls to examine whether there is a sex-biased predation rate. During their reproductive period, owls habitually accumulate dead prey items in the nesting cavity (Källander and Smith 1990, Roulin 2004) and the sex of these remains can be determined by visual inspection. For this study, we selected two owl species, the barn owl *Tyto alba* which forages in open area and the tawny owl *Strix aluco* which primarily hunts in forests. For both species we determined the sex ratio of their five predominant prey species over a period of approximately 10 years.

The common vole *Microtus arvalis* was the most common prey species found in nests of the barn owl. The other common prey were *Apodemus* spp. Because *A. sylvaticus* and *A. flavicollis* could not always be differentiated on the basis of the remains found in the nest, we lumped data of these two species and give the sex ratio data under the category *Apodemus* spp. We also found that species of the genus *Apodemus* were very common prey of the tawny owl. In addition, the two other common prey species were the bank vole *Clethrionomys glareolus* and the blackbirds *Turdus merula*. Only very few *Microtus arvalis* were found in nests of the tawny owl. The sex ratio of the four mammal prey was significantly male biased (number of males/number of females: range 1.26 to 2.13, Table 1). The most extreme departure was found for the blackbird where males accounted for 92% of the individuals preyed upon (Table 1).

A survey of the literature revealed that sex ratio bias during predation is very common. We found data for 11 bird species and all of them exhibited preferential probabilities to catch prey of a given sex. Overall, the departure from equal sex ratio was significant for 27 of the 32 prey species identified, and sample sizes were relatively small for the 5 cases with no significant deviation from equal sex ratio (the number of prey sexed ranged from 6 to 24 only). In the vast majority of cases (26 out of 29) with a significant sex ratio bias, the sex ratio of prey was male-biased.

We also found data about the sex ratio of prey of two mammals (Table 1). In both cases the sex ratio of the prey deviated from a 1:1 ratio. In one case the sex ratio was significantly male biased while in the other it was significantly female biased (Table 1).

Altogether these data support the view that sex-biased mortality induced by predation is a general phenomenon. Importantly, it appears that birds con-

sistently are more likely to prey upon males than females. There are several possible explanations for this pattern. First, males are more conspicuous in colour or size than females in many species. However, this is unlikely to be an important factor for predators as owls since they prey at dusk and dawn thus reducing the effect of colour dimorphism on predation rate. Moreover, among the prey found in the owl nests only *T. merula* exhibits a sexual dimorphism in colour. Second, males may behave differently than females (e.g. exhibit a greater tendency of males to disperse in mammals) which might result in greater exposure to predators. Thus, females of small mammals are often hidden with pups in their burrow while males actively defend their territory against conspecifics or predators. Furthermore, in most mammals males have a greater home range than females, and should be more easily detected and caught by predators when they display and contest with other males (Norrdahl and Korpimäki 1998). Similarly, blackbird males significantly increase their exposure to predators while singing at dusk and dawn during the reproductive season. Third, males may be less able to escape predators as a result of a higher parasitic infection rate due to a higher testosterone level and decreased immune function (Moore and Wilson 2002).

The higher predation rate by birds on males may have important implications on ageing rate and other sex-specific life-history traits in species which are mostly preyed upon by birds. According to classical evolutionary theories, lower extrinsic mortality should translate into a later onset of senescence (Medawar 1952, Williams 1957). Thus, the lower predation rate on females should select for slower female senescence and higher maximum lifespan compared to males. However, the predictions become more complex if mortality rates vary across age classes or if predation slows the rate of population growth and influences food availability (Abrams 2004). Indeed, if higher male mortality stems from behavioural activities associated with sexual display, territory defence and dispersal, as suggested by Table 1, it is likely that sex-specific differences in mortality rates will vary across age classes (Sibly et al. 1997). This could be directly tested by comparing the relative mortality rates of males and females between different age classes (Catchpole et al. 2000) or indirectly by comparing relative mortality rates during and outside the reproductive season. Such data would be very useful to unravel the apparent discrepancies between the predicted and expected patterns of senescence that have been observed in some species (Catchpole et al. 2004, Reznick et al. 2004).

The data we found in the literature does not allow us to determine whether mammalian predators are more likely to prey on males or females. It has been suggested

Table 1. Number and sex ratio (males:females) of prey remains found in nests, in dens or in pellets of different predator species. Type: O: observation of record kills; D: prey remains in dens; N: prey remains in nests; P: prey remains in pellets. For barn owl (*Tyto alba*), prey remains were sexed between 1990 and 2004 in 631 broods and for tawny owl (*Strix aluco*) between 1997 and 2005 in 394 broods from a population located in western Switzerland. P-values of binomial tests are given.

Predators	Prey Birds	Type	Males	Females	Sex ratios	P-value	Reference
Strix aluco	*Turdus merula*	N	36	3	12	<0.001	present study
Aegolius funereus	*Carduelis flammea*	N	3	5	0.6	1.0	Korpimäki 1981
	Fringilla montifringilla	N	3	3	1	1.0	Korpimäki 1981
	F. coelebs	N	47	10	4.7	<0.001	Korpimäki 1981
	Emberiza citrinella	N	12	1	12	0.006	Korpimäki 1981
Falco peregrinus	*Waterfowls (6 species)*	N	18	1	18	<0.001	Cade 1960
	Philomachus pugnax	N	48	16	3	<0.001	Lindberg 1983
Vulpes vulpes	*Anas platyrhynchos*	D	44	166	0.26	<0.001	Johnson and Sargeant 1977
	Mammals						
Panthera leo	*Tragelaphus strepsiceros*	O	207	143	1.45	<0.001	Owen-Smith 1993
Tyto alba	*Microtus arvalis*	N	1421	974	1.46	<0.001	present study
Aegolius funereus		N	32	14	2.29	0.012	Korpimäki 1981
Falco tinnunculus, Buteo buteo, Circus cyanus		P	1175	594	1.98	<0.001	Halle 1988
Aegolius funereus	*Microtus agrestis*	N	24	11	2.18	0.04	Korpimäki 1981
Aegolius funereus		N	2326	746	3.11	<0.001	Koivunen et al. 1996
Tyto alba		P	80	42	1.90	<0.001	Brown 1971
Tyto alba		N	168	16	10.5	<0.001	Taylor 1994
Aegolius funereus	*M. rossiaemeridionalis*	N	623	270	2.31	<0.001	Koivunen et al. 1996
Circus cyaneus, Ardea herodius	*Microtus townsendi*	P	97	65	1.49	<0.001	Beacham 1979
Bubo virginianus	*Microtus montanus*	P	9	31	0.29	<0.001	Longland and Jenkins 1987
Falco tinnunculus	*Microtidae*	N	16	3	5.33	0.022	Korpimäki 1985
Tyto alba	*Clethrionomys glareolus*	P	195	143	1.36	0.005	Brown 1971
Strix aluco		N	164	77	2.13	<0.001	present study
Aegolius funereus		N	208	61	3.41	<0.001	Korpimäki 1981
Aegolius funereus		N	1586	743	2.13	<0.001	Koivunen et al. 1996
Tyto alba	*Apodemus* spp.	N	858	662	1.30	<0.001	present study
Strix aluco		N	463	368	1.26	<0.001	present study
Falco tinnunculus, Buteo buteo, Circus cyanus	*Apodemus sylvaticus*	P	217	128	1.69	<0.001	Halle 1988
Tyto alba	*Mus musculus*	P	13	79	0.16	<0.001	Dickman et al. 1991
Aegolius funereus		N	8	4	2	1.0	Korpimäki 1981
Aegolius funereus	*Micromys minutus*	N	15	9	1.67	1.0	Korpimäki 1981
Bubo virginianus	*Peromyscus maniculatus*	P	15	43	0.35	<0.001	Longland and Jenkins 1987
	Dipodomys ordii	P	9	5	1.2	1.0	Longland and Jenkins 1987
Aegolius funereus	*Sorex araneus*	N	81	55	1.47	0.031	Korpimäki 1981
Aegolius funereus		N	240	194	1.24	0.031	Koivunen et al. 1996

that mammalian predators may frequently kill more females because they use odour cues to locate the nest or burrow which commonly are more likely to contain females than males (Johnson and Sargeant 1977, Norrdahl and Korpimäki 1998). If this was true, one would predict that opposite pattern of senescence between sexes for species whose main predators are mammals exhibiting a female biased rate of predation.

In conclusion, this survey reveals a large and pervasive sex ratio bias of prey species collected by different predator species. This bias in predation rate most likely stems from sex-specific differences in the prey behaviour, with males engaging in sexual displays and other activities that increase their probability of being preyed upon. Inversely, females might sometimes be more likely to be preyed upon, for example when female mallards incubate their eggs (Johnson and Sargeant 1977). These differences in predation rates are expected to affect the rate of senescence and other life history traits. These findings warrant additional studies to precisely determine how and why males are more frequently preyed upon than females, how the rate of predation varies between age classes and whether there are seasonal variations for sex specific differences in predation. The unusual predation behaviour of owls provides an ideal system to address these questions.

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