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REVIEW ARTICLE

BIRD PREDATION ON SPIDERS: ECOLOGICAL MECHANISMS AND EVOLUTIONARY CONSEQUENCES

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ABSTRACT. Birds are common predators of arthropods in many ecosystems but their impact on spiders has not been assessed. Therefore, the experimental evidence for bird predation effects on spider populations was examined. In particular, the present review focuses on the questions: what are the ecological mechanisms and what are the evolutionary consequences? Data from 17 field experiments, mainly in forest ecosystems, showed that spider communities were often significantly affected by bird predation. Comparisons of experimental effects were based on the ratio of mean density on experimentally enclosed vegetation and on controls. In 27 tests, a significant effect was detected (mean ratio 3.03) but in 9 tests the effect was non-significant (mean ratio 1.03). Furthermore, field experimental studies on bird predation effects on certain spider species or certain genera were reviewed. In three investigations, significant predation effects were found on agelenid, linyphiid and theridiid spiders but there were no significant effects on lycosids. Selective bird predation on large individuals has been shown in studies on spider communities and single species. Data on bird predation effects on species richness were lacking although impact on large species was expected to be important. Three field experiments showed that different spider families may experience differences in bird predation pressure. An aviary experiment showed that frequently moving spiders had a higher risk of predation than sedentary individuals, but the evidence from field experiments supporting the hypothesis of high predation pressure on moving spiders was limited. This included sex-specific differences in size and movement, although at least one experiment showed that males had higher winter mortality than females. One experiment showed that bird predation can affect anti-predator behavior. In conclusion, the present evidence showed that bird predation on spiders in several contrasting forest ecosystems is strong. However, there are many hypotheses regarding bird predation on spider populations that should be examined in future field experiments.

Keywords: Avian predation, field experiments, natural selection, spider community

Birds in terrestrial habitats consume insects and other arthropods in large quantities. This fact has recently led a number of authors to emphasize the importance of bird predation as part of the ''ecological services'' that human societies rely upon (e.g., Sekercioglu et al. 2004; Fayt et al. 2005; Sekercioglu 2006). Many studies have focused on the economic importance because of the large values that can be gained by reduction of insect herbivore populations in agricultural areas or managed forests (Takekawa & Garton 1984; Mols & Visser 2002). However, insectivorous birds are often generalists and may feed on many trophic levels. This means that birds are not only eating herbivores that are damaging human food or other resources, but also include in their diet arthropods (e.g., spiders) that otherwise compete with birds for insect prey.

Arachnologists have long acknowledged birds as a potential threat against spider populations but they have had different opinions about their importance. In the first edition of ''Biology of Spiders'' Foelix (1982) stated that ''The influence of birds as a factor controlling spider populations is generally overestimated.'' He argued that spiders often hide, sit motionless, are cryptic, or are active during the night and, therefore, spiders would be poorly perceived by birds. Moreover, he said that adult birds rarely eat spiders but certain species may feed spiders to their young. There were no references to support these claims. In the second edition, Foelix (1996) added that ''spiders are a major prey for many birds during winter'' and referred to the works by Askenmo et al. (1977) and Hogstad (1984). Thus, results from experimental studies have gradually been

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accepted in textbooks but still much of the data referred to are from old, mainly descriptive studies. Wise (1993) in his book on spider ecology discussed birds as important natural enemies of spiders and referred to several experimental works. He concluded ''birds take substantial numbers of overwintering spiders from spruce branches, and birds have been implicated as important predators upon large orb weavers in tropical forests.'' Thus, in this book birds are rated among the most prominent predators on spiders. However, in more recent papers, authors have questioned whether birds really are important as mortality agents (e.g., Blackledge et al. 2003).

The present review is not intended to be an exhaustive evaluation of all papers discussing the importance of birds as predators on spiders or their egg-sacs. There have been many conclusions about the effects of bird predation on spider populations based on rather poor data or interpretations that go beyond the data at hand. Instead, the focus in the present paper will be on the experimental evidence for the impact of birds on spiders in natural populations. Experiments in field ecology have become increasingly popular as a way to examine hypotheses about predation in different habitats (Hairston 1989). Many of the conclusions in Wise's (1993) book on spider ecology were based on experimental evidence. The experimental approach has certain advantages. Experiments provide good insights into cause and effect and are a means to test hypotheses. This approach may also help to disentangle complex interactions in natural habitats. It was in the 1970s that field experiments of bird predation on spider populations became well established in the ecological literature (e.g., Askenmo et al. 1977; Holmes et al. 1979). These pioneering experiments and their successors will be the focus of the present review.

Two questions of importance will be highlighted: what are the ecological mechanisms of bird predation on spiders, and what are the evolutionary consequences? In a previous review of bird predation on arthropods, Holmes (1990) emphasized these two functions of bird predation. First, I will present some work on birds' diets. Second, experimental studies on bird predation effects on spider assemblages will be scrutinized. Third, investigations of bird predation on single species are reviewed. Fourth, the importance of birds as selective agents on spider populations is summarized. Finally, bird predation on spiders is evaluated in an ecological and evolutionary context and this also leads to new hypotheses.

SPIDERS AS BIRD PREY

Bristowe (1941) referred to several field observations of birds eating spiders, especially in investigations on the effect of birds on pests, in the early 20th century. However, the importance of spiders as prey of birds has mainly been supported by analyses of stomach contents and fecal samples. In his review of spider enemies, Bristowe (1941) evaluated the importance of bird predation as a mortality agent of spiders mainly by using data from stomach analyses. The stomach data were used to estimate average numbers of spiders eaten by various bird species suggesting, e.g., that a blackbird would eat 106 spiders per year. In further calculations, various assumptions and rough estimates about population sizes of birds and spiders led to the conclusion that birds in England and Wales did not pose a serious ''threat'' to spider populations (Bristowe 1941). In terms of population dynamics this means that Bristowe suggested that birds did not control (regulate) spider populations.

Stomach analysis has often been used to identify the number of individuals of various prey items. For instance, in a quantitative examination of prey of goldcrests (*Regulus regulus*) in winter, Hogstad (1984) suggested that, on average, 60% of the individual prey were spiders. In mid-winter (January and February) the percentage increased to about 80%. On the other hand, spiders can be quite rare in other birds' diets. In an analysis of the stomachs of the meadowlark (*Sturnella magna argutulla*) in Florida, Genung & Green (1974) found a few remains of lycosids in 12.7% of 63 birds examined.

Another possible approach was to examine fecal samples. The feces were easier to sample and the sample size could often increase considerably in comparison to stomach samples. It was also convenient because birds were not harmed by sampling. For instance, in a study of the threatened California gnatcatcher (*Polioptila c. californica*), fecal samples showed that the adult gnatcatchers selected more and larger prey, including spiders, to feed their chicks than adult birds ate themselves (Burger et al. 1999). However, there was constantly a

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risk that estimations of prey numbers would be biased. In a study of the diets of the willow tit (*Parus montanus*) and crested tit (*P. cristatus*), Jansson (1982) showed that numbers of spiders and beetles were overestimated in fecal samples in comparison with estimates of prey brought to the nest by using color photographs from cameras at the nest entrance.

Both stomach analysis and fecal samples have a number of important limitations when assessing the importance of bird predation. First, the digestion of prey makes it difficult to correctly assess the numbers of various prey taxa. It is true that many arthropods have distinctive sclerotized body parts but still it could be hard to provide counts of individuals based on different numbers of cheliceral fangs, tarsal claws, leg parts, etc. Second, biased data will lead to incorrect estimates if it is magnified several times. Samples including a few bird individuals will not be sufficient for an unbiased estimate of the predation pressure on the arthropod prey. Third, the relevance of bird predation on spider populations is dependent on local abundance and this is usually unknown in studies based on ingested food. If the population size of the spiders is rather small but increasing, then relatively moderate predation pressure can cause a significant decline of spiders locally. On the other hand, even high predation pressure by birds would not influence an extremely large population to any significant extent. These types of interactions between birds and their arthropod prey have been observed in several study systems in forests (e.g., Crawford & Jennings 1989; Holmes 1990). Different spider populations probably show a similar response to varying bird predation pressures. In order to evaluate the importance of bird predation on local spider populations, some estimate of the effect of the predation must be made, preferably by comparing data on spiders exposed to birds vs. spiders protected from bird predation.

BIRD PREDATION ON SPIDER ASSEMBLAGES / COMMUNITIES

Studies on spider assemblages, or communities, offer good opportunities to evaluate the impact of bird predation. The advantages of such studies are that it is usually easier to study the effects of manipulated bird predation pressures on entire communities than single species. The response is the sum of all spiders which means that even small effects on individual species are combined into the observed grand mortality. There were several experimental field studies of bird predation on arthropod populations in contrasting habitats between 1977 and 2007 (Table 1). In certain of these experiments the focus was on spider populations and in others, in which many arthropod taxa were studied, the results for spiders were reported separately.

Methods.—All the studies employed experimental methods using different types of exclosures to prevent birds from foraging. Typically, the exclosures covered some part the vegetation in which spiders and other arthropods were dwelling. Nearly all studies utilized nets with coarse mesh size (10–58 mm) so that arthropods were free to leave and enter the exclosures without restrictions. Possibly some large arthropods such as adult butterflies may have been hindered in their movements by the netting, but in general the authors considered such effects as negligible. In a few cases, fine mesh size (1×1 mm) was used but those experiments were performed during the winter when movements of spiders and their prey are usually minimal.

A factor that usually is not controlled for in most of the experiments concerns the introduction of an additional structural component to the habitat in the form of the net. This is a classical problem in exclosure experiments in other habitats and taxa (Hairston 1989). The primary disturbance caused by addition of the extra net-structure may be to support more web building spiders (Rypstra 1983; Greenstone 1984). This could increase the carrying capacity of spider populations if there is shortage of sites for attaching webs in the study habitat (Robinson 1981; Greenstone 1984; Wise 1993; Rypstra et al. 1999). However, there are reasons to believe that the bias due to the extra net-structure is rather weak. First, nearly all experiments have been performed in trees or bushes with abundant foliage (including leaves, needles, branches, twigs etc.) for attaching webs. There is, therefore, no reason to expect that structure in itself is limiting in the studied habitats, but it would be highly welcome if appropriate controls using sheets of netting (without enclosing the foliage) were included in future experiments. However, in at least one experimental study the authors used procedural

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Table 1.—Field experimental studies of bird predation effects on spider assemblages. The experimental effect is shown as the ratio of density of spiders in experimental units to control units. Significance levels shown as * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$) or NS (not significant).

Habitat	Experimental season / country	Methods	Population estimate	Experimental effect: density experimental unit / density control unit	Reference
Coniferous forest (*Picea abies* trees)	Winter: October–March / Sweden	Net-enclosures: coarse (10 mm) and fine (1 mm) mesh size	No. per kg branch-mass	Coarse mesh size: 3.01 ** Fine mesh size: 1.54 *	Askenmo et al. (1977)
Broadleaf forest (understory shrub)	June–August / New Hampshire, USA	Net-enclosures (mesh size 22 mm)	No. per 400 leaves	0.96 NS	Holmes et al. (1979)
Coniferous forest (*Picea abies* trees)	Winter: October–March / Sweden	Net-enclosures: fine (1 mm) mesh size	No. per kg branch-mass	2.67 **	Gunnarsson (1983)
Temperate broadleaf forest (Pennsylvania), subtropical (Peru) & tropical forest (Gabon)	26 days experimental period, various seasons / USA, Peru, Gabon	Cages: coarse mesh size, Penn.: 30 mm (chicken wire), Peru & Gabon: 30-50 mm (sticks)	No. in experimental plots	Penn. Day: 1.20 NS, Night: 1.01 NS Peru, Day: 2.37 *, Night: 1.32 NS Gabon, Day: 1.60 *, Night 1.23 NS (survival of exp. spiders)	Rypstra (1984)
Sagebrush (*Artemisia tridentata*) up to 2 m	13 months: June 1982–July 1983 / Oregon, USA	Cages (25 mm mesh size)	No. per plant	1.64 *** (both experimental & control first defaunated)	Wiens et al. (1991)
Coniferous forest (*Picea abies* trees)	23 months: April 1989–March 1991 / Sweden	Net-enclosures: coarse (10 mm) mesh size	No. per kg dry branch-mass	Summer-89: 1.82 NS Winter-90: 3.77 *** Summer-90: 2.17** Winter-91: 2.34***	Gunnarsson (1996)
Salix shrubs	June–September / Finland	Cages, mesh size 22 mm	No. per leaf area	? NS	Sipura (1999)
Broadleaf forest (*Quercus* & *Betula* trees)	May–September / Sweden	Net-enclosures: coarse (10 mm) mesh size	No. per kg leaf mass	Oak*** site A: 1.58, site B: 6.06, site C:7.84 Birch*** site A: 5.89, site B: 8.93, site D: 3.09	Gunnarsson & Hake (1999)
Coffea arabica (shrubs, "dwarf hybrids")	January–May / Guatemala	Net-enclosures: coarse (58 mm diagonal size) mesh size	No. per 100 g foliage	2.18 **	Greenberg et al. (2000)
Eucalyptus calophylla (saplings < 3 m)	12 months: May 1997–May 1998 / Australia	Cages, mesh size 25 mm	No. per plant	August-97: 2.35 ** October-97: 2.50 ** May-98: 3.74 ***	Evelegh et al. (2001)

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Table 1.—Continued.

Habitat	Experimental season / country	Methods	Population estimate	Experimental effect: density experimental unit / density control unit	Reference
Metrosideros trees, 2–3 m tall	33 months: August 1998–May 2001 / Hawaii	Cages, coarse mesh size (20 mm)	No. per 100 g foliage	0.82 NS (excluding one abundant, invasive sp)	Gruner (2004)
Inga spp, branches 3–4 m above the ground	Dry season: February–April Wet season: May–July / Mexico	Net-enclosures, coarse mesh size (35 mm)	No. per gram dry foliage	Dry season: 3.00 *** Wet season: 1.80 ***	Philpott et al. (2004)
Canopy, 30–40 m, e.g. *Anacardium excelsum, Brosimum utile, Manikara bidentata.* Understory, ≈ 1.2 m	11 months: April 2000–March 2001 / Panama	Enclosures, coarse mesh size (20 mm)	No. per m^2 leaf area	Site 1: Canopy, Wet 2.00 ***, Dry 1.60 * Understory, Wet 0.80 NS, Dry 1.10 NS Site 2: Canopy, Wet 0.85 NS, Dry 1.10 NS Understory, Wet 1.15 NS, Dry 0.60 NS	Van Bael et al. (2003) Van Bael & Brawn (2005)
Pinus trees, 1–3 m tall	27 months: June 1999–September 2001 / Colorado, USA	Cages, coarse mesh size (25 mm)	No. per tree	Hunting spiders: 1.25 * Web-spinning spiders: ? NS	Mooney & Linhart (2006)
Pinus trees, 4.5–13.5 m tall	June to September / Colorado, USA	Net-enclosures, coarse mesh size (25 mm)	Biomass estimate (mg dry spider / kg branch mass)	Hunting spiders: ? (biomass–38%) NS Web-spinning spiders: ? NS	Mooney (2006)
Eucalyptus saplings, ≤ 2.8 m tall	20 months: October 1998–May 2000 / Australia	Net-enclosures, coarse mesh size (35 mm)	No. per sapling	Nov-98: 2.05 * March-99: 2.06 * June-99: 1.77 *** Nov-99: 2.54 *** Feb-00: 2.51 *** May-00: 1.60 *	Recher & Majer (2006)
Pinus trees, branches 0.5–6.0 m above the ground	14 months: June 2001–August 2002 / Colorado, USA	Net-enclosures, coarse mesh size (25 mm)	Biomass estimate (mg dry spider / kg branch mass)	Hunting spiders: ? (biomass–24%) * Web-spinning spiders: ? NS	Mooney (2007)

controls (Van Bael & Brawn 2005). These dummy exclosures had open sides that allowed birds to forage in the foliage. There was no indication that the dummy exclosures attracted arthropods, or reduced the light. Second, birds could always reach spiders sitting in their retreats or on their webs attached to the outside or on the inside of the cage or net. This ability of birds to reach spiders just inside the exclosure, of course, depends on mesh size but nearly all studies have used a coarse mesh size which should be penetrable by bills of insectivorous birds. If spiders prefer to place their webs close to the net this could lead to an underestimate of bird predation pressure. Third, in some of the studies the effects of extra net-structures were possibly minimized by a long experimental period. For instance, if the study was performed in temperate or boreal zone with cold winters, interaction between the net-structure and spiders is probably minimal during cold periods.

The database on bird predation effects.—The studied habitats are mainly forests in different successional stages with shrubs and trees as experimental units. Coniferous trees as well as broadleaf species have been examined. Three studies were from coniferous forests in southern Scandinavia with *Picea abies* as the predominant tree (Askenmo et al. 1977; Gunnarsson 1983, 1996). The investigations focused on branches in the lower part of the canopy (up to 4 m above the ground) that were reached by using a transportable platform. Spider densities were related to the branch-mass. Three studies in Colorado were also in coniferous forest. In one case, the samples were all from rather small *Pinus* trees, not taller than 3 m (Mooney & Linhart 2006). In the other experiments, pines were between 4.5 and 13.5 m tall (Mooney 2006, 2007). The spider densities were measured as number of animals per tree (Mooney & Linhart 2006), or biomass per branch (Mooney 2006, 2007).

One early study on bird predation on arthropods was done in a broadleaf forest in New Hampshire (Holmes et al. 1979). However, the experiment was performed in understory shrubs (*Acer pensylvanicum*). In Northern Europe, Sipura (1999) investigated bird predation effects in *Salix* shrubs and Gunnarsson & Hake (1999) examined arthropods on branches in canopies of *Quercus* and *Betula* trees. A ''sky-lift'' was used to sample up to 6 m above the ground. In these studies, spider densities were related to number of leaves, leaf area, or leaf mass.

In five studies, moderately high trees were used for experimental purposes. Saplings of *Eucalyptus* spp. up to a height of 3 m were sampled in Australia (Evelegh et al. 2001; Recher & Majer 2006) and in these cases the number of arthropods was counted per sapling without compensation for size differences. Other investigations were done in coffee plantations, either in shrubs of *Coffea arabica* (Greenberg et al. 2000) or in branches of *Inga* trees 3–4 m above the ground (Philpott et al. 2004). In Hawaii, spider populations in 2–3 m tall trees of *Metrosideros* were examined for bird predation effects (Gruner 2004). The densities of spiders in these three studies were related to the mass of foliage.

One study was done in several rain forests in Panama (Van Bael & Brawn 2005). The height of the tree top canopies varied between 30 and 40 m above the ground and in some of the sites the predominant tree species were *Anacardium excelsum, Brosimum utile* and *Manilkara bidentata*. The tree tops were reached by using canopy cranes with a 50-m tower that had a gondola attached to a boom. In this way, the investigators could reach tree branches on all heights and each crane covered between 0.70 and 0.88 ha of the forest canopy. The arthropod densities were estimated as numbers per leaf area.

One of the studies was performed in open land in Oregon. In this experiment, plants of *Artemisia tridentata* were manipulated to examine the effects by bird predation and plant chemistry (Wiens et al. 1991). Finally, Rypstra (1984) conducted an experiment with a standardized number of spiders placed in the vegetation of a broadleaf forest in temperate, subtropical, and tropical environments. The disappearance rates of spiders were used for comparison between treatments.

The studies ranged over five geographic regions. There were five experiments performed in Northern Europe (Sweden and Finland), five in North America (New Hampshire, Oregon, and Colorado), three in Central America (Mexico, Guatemala, and Panama), one in Hawaii and two in Australia. In addition, one experiment was performed on three continents (USA, Peru, Gabon).

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Five of the studies were long-term with an experimental period over 12 months and another study continued for 11 months. These investigations covered at least an annual cycle and this means that the data were not the result of a temporary predation effect. The seasonal variation in bird predation pressure could potentially be large because of variation in bird density (e.g., seasonal migration) or intensity of foraging (e.g., raising hatchlings). It has also been proposed (Askenmo et al. 1977) that bird predation could be strong during the non-breeding season because of non-favorable climate in winter. This means that non-migratory birds have to increase their efforts of finding food in winter to meet their energy demands (e.g., Norberg 1978). Some of the studies focus on the winter situation, or the dry season, and the effects on prey populations. Other studies were short-term experiments focusing on the direct effects on arthropods during summer, or the breeding season.

Experimental results at the community level.—Summarizing the data in Table 1, it can be concluded that bird predation often significantly reduces spider densities. Comparisons were based on the ratio of mean density on experimentally enclosed vegetation and controls without such restrictions. Data showed that spider densities on plants protected from bird foraging significantly exceeded controls in ratios between 1.25 and 8.93. The mean ratio for experimental tests with a significant effect was 3.03 (SD 1.93, $n = 27$). This estimate includes more than one test in each paper because many of the experiments reported were divided into separate investigations on different tree species and sites, etc. The studies included could be regarded as independent tests, although in some cases data were analyzed in an overall ANOVA. The mean ratio in tests with a non-significant result was 1.03 (SD 0.35, $n = 9$). Six studies, however, could not be included in the density ratios. Two studies (Rypstra 1984; Wiens et al. 1991) were not included because of the experimental design (see below), and in two cases it was not possible to calculate any ratio because no data were presented (Sipura 1999; Mooney & Linhart 2006). Finally, in two studies, there were no density estimates provided; instead the biomass was estimated from spider length distributions (Mooney 2006, 2007).

The data taken together could be used for a rough estimation of the percentage of experimental tests that resulted in significant effects of bird predation on spider densities. A study that reported the most dramatic effect (25–80-fold increase) was excluded because it focused on a single, invasive species (Gruner 2005). Overall, 63% of the tests indicated a significant reduction in densities of spider communities. This suggests that bird predation could be regarded as a potentially important mortality agent.

It should be noted that nearly all experiments examined report on bird predation effects in forest ecosystems or in habitats with dense vegetation of bushes, often including at least a few trees. Only Wiens et al. (1991) reports on bird predation in an open habitat with sagebrush (*Artemisia tridentata*). This could be explained in two ways: either there have been few experiments performed in open habitats, or the experiments have mostly produced non-significant results that have been difficult to publish in refereed journals. It is, of course, also possible that a number of studies performed in forest habitats have remained unpublished because they did not show any significant results. However, several studies have focused on the effects on the arthropod populations in the study habitat. This means that a large number of taxa are often analyzed, some groups showing a significant response to bird predation others showing no significant response. Possibly, this type of experimental study, which includes several arthropod taxa, reduces the risk of ''hiding'' non-significant results, because a significant effect by birds on at least one arthropod group often justifies publication. In published studies, spiders are often among the taxa that are numerically affected by birds. In some experiments, bird predation effects were detected in spiders but not in other arthropods, or in few other taxa. For instance, Evelegh et al. (2001) examined the effects of bird predation on 19 different arthropod orders of *Eucalyptus* saplings but they only found evidence for a significantly higher density of spiders in net-protected canopies. On the other hand, Gunnarsson & Hake (1999) found that bird predation negatively affected arthropod abundances in six out of nine orders (including spiders) examined in birch (*Betula pendula*) and oak (*Quercus robur*) canopies.

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The experimental studies by Rypstra (1984) on predation (predominantly by birds) on web-building spiders in three continents, and by Wiens et al. (1991) of bird predation on arthropods in sagebrush (*Artemisia tridentata*) were not included in the mean value of predation effects reported above. The reason for excluding them is that the comparison was not based on control vs. experimental density. In Rypstra's study (1984), a fixed number of spiders (240 individuals in four groups in each of the study sites) were placed in forest sites and their survival during 6-h periods was measured. Thus, there was no estimation of the natural density, or the effect on the spider community. However, Rypstra (1984) could show that the relative disappearance rate of spiders was higher during the daytime than at night at the Peru (subtropical forest) and Gabon (tropical forest) sites but not at the site with temperate forest in the USA. She concluded that predation by vertebrates (most likely birds) was significant on web-spiders during the daytime in subtropical and tropical sites.

Wiens et al. (1991) used an approach that differs from all other experiments reported on here; i.e. arthropods were first removed from shrubs and the recolonization of different taxa on caged or exposed shrubs was observed. No exact calculations for arachnids were given in the text. However, raw data provided in the paper's Appendix 1 could be used to assess the importance of bird predators on the abundance of spiders on sagebrush. The relevant comparison is the one between shrubs that were caged and open shrubs because both types of shrub were defaunated at the same time and the only difference was caging. Wiens et al. (1991) used several sub-experiments in their design and the longest experimental period was 56 weeks. The mean value for caged shrubs after 56 weeks was 1.89 spiders and for open shrubs the mean was 1.15 spiders. This difference was significant ($P < 0.001$) using a *t*-test. Consequently, the experimental result supports the hypothesis that birds affect the abundance of spiders in sagebrush.

BIRD PREDATION ON SINGLE SPECIES

Studies of ecological mechanisms can be difficult to perform on communities because the various species respond in very different ways. Therefore, experimental investigations on bird predation effects on single species may reveal how the predation affects life-history traits. There are few studies focussing on the effects of bird predation on a specific spider species or genus. Here, I will review four studies that employ experimental methods. The first study concerns the funnel-web spider *Agelenopsis aperta* (Gertsch 1934) in two distinct habitats in Arizona (Riechert & Hedrick 1990). The funnel functions as a retreat that protects the spider from predatory attacks.

The two study sites included a desert grassland and a riparian habitat in woodland, respectively. In their study, Riechert & Hedrick (1990) estimated predation rates on *A. aperta* in two ways. First, in each study site an area of 900 m^2 was enclosed with sheet metal flashing. All spiders in webs were marked and pitfall traps at regular intervals inside and outside the metal flashing made it possible to detect migrating individuals that were marked and released on the opposite side of the metal flashing. Second, a field experiment was performed by protecting certain webs from bird predation by means of netting. The survival of individuals at protected webs was compared with those at unprotected webs in 1-week periods.

In the population monitoring, the losses of individuals differed significantly between the habitats. In the riparian site, spiders disappeared at a rate of 63% to 72%. However, in the grassland area, the disappearance rate varied between 4% and 10%. The experimental exclusion of bird predation resulted in large differences in disappearance rate (30% and 51% difference per year) between protected and unprotected webs in the riparian habitat, with higher survival of spiders in protected webs. In the grassland habitat, there were no significant differences in spider survival at protected and exposed webs. Consequently, bird predation on *A. aperta* seemed to be important in the riparian habitat but no measurable effect could be found in the grassland. Riechert & Hedrick (1990) also referred to a study by Greene (1989) that reported significant bird predation effects on canopy-living spiders in a pine habitat adjacent to their riparian habitat.

Vertebrate predation on two species of lycosids, *Schizocosa ocreata* (Hentz 1844) and *S. stridulans* Stratton 1984 was studied in an exclosure experiment in secondary forest in Kentucky (Wise & Chen 1999) over two years. These wolf spiders were very common on

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the floor of forests dominated by oak and maple and > 90% of lycosids in the study site belonged to the genus *Schizocosa*. Birds and other potential vertebrate predators, such as shrews, were common in the experimental plots. In late spring, five locations were established. In each location, two 50 m^2 areas were selected at random as a "removal-exclusion" treatment, or as "open reference." Vertebrates inside each exclosure were trapped and removed. The density estimates of *Schizocosa* included all stages and the analysis was based on eight samples during two years.

The removal of vertebrate predators, including birds, did not affect lycosid densities. The treatment factor (i.e., the exclosure) approached $P = 0.10$ in an ANOVA but *Schizocosa* densities tended to be higher in the "open reference" plot rather than the protected one. Wise & Chen (1999) suggested that the removal of vertebrate predators might cause an increase in the density of another, unknown major arthropod enemy of *Schizocosa* that depressed the lycosid density. However, they emphasized that this was a speculative suggestion.

In a study during two years, the effects of bird predation on the linyphiid *Pityohyphantes phrygianus* (C.L. Koch 1836) was examined by manipulation of predation pressure (Gunnarsson 1993, 1998). This sheet-web spider lives on branches of coniferous trees and it is exposed to predation by passerine birds during all stages of the biennial life cycle. Many of the bird species are non-migrating and they form multi-species flocks that patrol the same area during overwintering.

The results were part of an experiment on bird predation effects on the spider community in spruce (Gunnarsson 1996). Randomly selected spruce branches between 1.5 and 4 m above the ground were enclosed in coarse-meshed nets (mesh size 10 × 10 mm) and other branches were left as controls. Four sampling periods, fall and spring in each of two years, were used and in all cases removal of bird predation significantly increased the density of *P. phrygianus*.

In the spring samples, i.e., after the winter period with a combination of bird predation and other, temperature related, mortality causes, the spider mean density of experimental, net-enclosed, branches was 4.1–10.5 times the mean of control branches (Gunnarsson 1993). In samples collected in the fall, the mean densities in net-enclosed branches were 2.3–2.6 times the densities of controls. The predation effects on males and females were similar in three out of four samples (Gunnarsson 1998). In the fall samples, the mean number of individuals for each sex on net-enclosed branches was 2.1–2.3 times the controls. A more pronounced difference between the two branch categories was found after the winter. The mean number of males on protected branches was 10.3 times the controls, and for females the effect was 10.6 times. However, in the second spring sample there was a sex-related difference in the bird predation effect. In males, there were 5.5 times more individuals on net-enclosed branches compared with control branches. In females, the predation effect was only 2.8 times more individuals on protected branches. These results suggest that bird predation can be sex-specific under certain circumstances and this will be discussed further below (see "Selective predation").

Another experimental study of bird predation was carried out on a theridiid spider, *Achaearanea* cf. *riparia* (Blackwall 1834) on the island of Hawai'i. This species is an exotic to the study site and it is presently expanding its distribution on several locations on the island of Hawai'i (Gruner 2005). The experimental site was a high altitude, wet forest in early succession and the vegetation was dominated by the tree *Metrosideros polymorpha*. Birds were common insectivores in the study site.

The results on *A. riparia* were part of a larger experiment that examined the relative influences of bottom-up and top-down effects in a Hawaiian food-web (Gruner 2004). Fifteen individuals of *A. riparia* were collected in total from 28% of the plots at the start of the study. However, at the end of the experiment, 939 individuals were collected in caged plots but only 22 individuals in control plots where birds could continue their foraging without any restrictions. If the abundance is expressed as spider density (No. per 100 g foliage), the mean density on caged trees was approximately 28 times the mean density on control trees. A closer look at the size distribution of *A. riparia* in the treatment groups suggests that large individuals benefited even more from exclusion of bird predation. The possible size selection by birds on spiders will be discussed now.

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SELECTIVE PREDATION

Bird predation pressure on spider populations can have consequences that are much more far-reaching than just a reduction of the local abundance. If bird predators select their prey with some sort of discrimination there will be unequal risks of being eaten depending on the phenotype of the prey. This will lead to a selective advantage to certain individuals and over time the frequencies of different phenotypes in the population will change due to bird predation. The prerequisites for such a process are (i) variation in the studied trait (size, color, etc.), (ii) a genetic basis for the trait, and (iii) fitness differences between individuals displaying the trait. When these conditions are fulfilled, natural selection occurs (Endler 1986).

There are several studies on birds acting as selective agents on their prey. Especially birds in forest ecosystem may have a large evolutionary impact on their arthropod prey (Holmes 1990). There are a number of studies of predation effects on spider populations that can be used to assess the importance of birds as selective agents. In reviewing these studies, I put special emphasis on the experimental evidence but in certain cases I also include investigations in which there are good reasons to assume bird predation as an important mortality factor.

Selection on size, sex and color.—One of the most obvious traits for selection is size. Theoretical models suggest, for instance, that size-specific predation pressure can affect the evolution of life history if the coupling between predator and prey is strong (Day et al. 2002). Size is an extremely important trait that affects many aspects of the life history of spiders and other arthropods. Data suggest that females of the agelenid *Agelenopsis aperta* can benefit in terms of fitness by mating with a large male (Riechert & Johns 2003). The offspring of females mated to large males were ''bolder'' and more aggressive than the offspring sired by small males. There are numerous studies showing that large males have a higher probability of winning contests with smaller opponents over females (see Elgar 1998 for examples). Moreover, in some species large males mature early and this is favored if there is protandry, i.e., males on average maturing before the females (e.g., Gunnarsson & Johnsson 1990). If there is first-sperm priority, which is common in many spiders (Elgar 1998), the males reaching the adult stage early will have a mating advantage. This could be achieved by enhanced growth rates and large size, which suggests that sexual selection is acting (Wiklund & Fagerström 1977; Gunnarsson & Johnsson 1990), but early maturation could also be associated with small size and fewer molts (Vollrath 1987). In addition, it should be noted that in many species there is obviously selection for small male size because of predation risk (e.g., Vollrath & Parker 1992). In female spiders, there is a general relationship between large size and fecundity (Vollrath 1987; Marshall & Gittleman 1994). This has been suggested as a major selective force for the evolution of size dimorphism exhibited in several spider genera, e.g., *Nephila* (Coddington et al. 1997). However, predation by visually hunting predators is potentially an important selective force acting against large size.

Experiments on bird predation effects on the entire spider population in a forest ecosystem have often revealed that there are differences in predation pressure on various size categories. For instance, in a coniferous forest in Sweden there was a significant decrease in population size by large spiders (body length $\geq$ 2.5 mm) but this was not found for small spiders during winter (Askenmo et al. 1977). In the same system, Gunnarsson (1983) found a significant decrease in the density of both small ($<$ 2.5 mm) and large ($\geq$ 2.5 mm) spiders during winter but bird predation pressure varied. A comparison of spring densities expressed as the ratio between experimental (branches protected from predation) to control mean density showed that for small specimens there was a 2.0-fold increase in density on branches protected from bird predation. The increase in the number of large specimens on protected branches was 6.1. This suggests that the predation pressure on large spiders was higher than on small ones.

In another experiment in a spruce (*Picea abies*) forest of southern Sweden, the mean (and median) size was significantly larger on branches protected from predation via exclosures (Gunnarsson 1996). The experiment started in spring and the first sampling was done in fall, five months later, and the second sampling was performed after the winter, six months after the first one. Another two samplings were executed in fall and spring with a six-month interval

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between. In all samplings, the mean size of spiders on branches protected from bird predation was significantly larger than on unprotected control branches. The mean size of spiders inside exclosures was 133% and 124% of the size on control branches exposed to predation in samples after the summer. In early spring, after the winter, the corresponding differences were 132% and 133%, respectively. Thus, removal of bird predation increased the mean size with 24–33%, suggesting that birds were selecting large-sized spiders as prey in both summer and winter. However, there was a reduction in mean size in control branches after winter in comparison to fall samples (2.42 to 1.79 mm and 2.29 to 1.87 mm).

In an exclosure experiment, Recher & Majer (2006) examined the effects of bird predation on arthropods in *Eucalyptus* woodland. The spiders were categorized into three size-classes (i.e., size-class 1: ≤ 2.0 mm, size-class 2: $> 2.0 \leq 4.0$ mm, size-class 3: > 4.0 mm) and densities inside and outside exclosures were compared six times during 1.5 years. In size-class 1, the densities were significantly higher on enclosed saplings than on controls in five out of six comparisons. In the two larger size-classes, 2 and 3, there were significantly higher densities in four out of six and two out of six comparisons, respectively. Overall, when averaged over the six samplings the ratios for densities on enclosed saplings over control branches of the size-classes 1, 2, and 3 were 2.2, 1.8, and 2.5, respectively. This suggests that bird predation effect was high in all size-classes, but low abundances and high variances, in particular in the largest size-class, resulted in few significant differences between experimental and control branches.

Studies on single species also show that birds are a stronger selective agent on large individuals in comparison with smaller individuals in *Pityohyphantes phrygianus* (Gunnarsson 1998). In a temperate forest, overwintering subadults that did not molt between the samplings in fall and spring in two years were examined in an experimental study. Large individuals survived better than smaller ones in both sexes and both years. In March each year, the mean size ratios of females on net-enclosed branches versus controls were 1.07 and 1.05, respectively. In males, the ratios were 1.09 and 1.02 (not significant), respectively. Consequently, passerine birds in the coniferous ecosystem studied seemed to catch disproportionately more large individuals of female and male *P. phrygianus* during winter.

In the invasive *Achaearanea* cf. *riparia* on the island of Hawai'i (Gruner 2005), comparisons of the total abundance of five size-classes suggested that the intensity of bird predation was lowest on the smallest size-class (individuals between 0.5 and 1.5 mm). There were no individuals larger than 3 mm found in control plots, whereas 34 spiders 4 or 5 mm long were collected within cages that protected *M. polymorpha* trees from bird predators. Given the few individuals collected in certain size-classes, no statistical test was performed. This means that the data are supporting the hypothesis that birds were size-selective, but no firm conclusion could be drawn.

Selection on size is closely related to sex-specific survival. Sexual size dimorphism is common in several families; e.g., Araneidae (Foelix 1996; Roberts 1996), and the evolution of spider size dimorphism has been much discussed (Vollrath & Parker 1992; Coddington et al. 1997; Vollrath 1998; Prenter et al. 1997, 1999). For instance, in web-builders it has been argued that males spend more time searching for females that are often sedentary in their webs. This means that the sexes may have differences in exposure time to visual predators and this could select for smaller size in the roving males (Vollrath & Parker 1992).

There are several studies indicating that males move around to a higher extent than do females of web-building spiders, but the experimental evidence of a higher predation pressure on males is meagre. Individuals of *Theridion grallator* Simon 1900 that moved around in forest habitats were caught on leaves coated with adhesive (Gillespie & Oxford 1998). From December through February only immatures were collected. In the period between March and August nearly all individuals were males but no mature female was caught at all. This suggested that males were more vagrant than females. However, females of web-builders in other species may move between different sites to change the location of the web. In the orbweaving *Tetragnatha elongata* Walckenaer 1842 the frequency of relocation depended not only on habitat quality (prey capture rates) but also on the distance travelled between the habitats (Gillespie & Caraco 1987). The distance moved at the site with few prey was 2.8 times the distance travelled at the site with high

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captures rates. However, there may also be sex differences in distance moved in free-hunting spiders. For instance, males of *Hogna helluo* (Walckenaer 1837) moved nearly 3 times further than females in a laboratory experiment (Walker & Rypstra 2003). However, such a difference was not found for *Pardosa milvina* (Hentz 1844).

The survival of males and females has been examined in certain spiders and the mortality rates could sometimes be related to predation by birds. An estimation of mortality in *Nephila clavipes* (Linnaeus, 1767) in Panama (Vollrath & Parker 1992) showed that roving males experience a much higher risk of death ($>$ 80% in 10 days) than females, subadults or juveniles, i.e. from $\approx$ 7% in 20 days in mature females to $\approx$ 30% in subadult females. There appears to be a switch in male mortality, from relatively low to considerably higher death rates, when they mature and start searching for sedentary females. Part of the lower survival of males is probably related to increased exposure to visually hunting predators such as birds. Moreover, moving in itself is risky and increases the probability that active spiders will be eaten by birds (Avery & Krebs 1984).

In *Pityohyphantes phrygianus*, experimental evidence from Scandinavian forests show differential mortality of the sexes. A combination of factors contributes to the skew in mortality rates. In a series of experiments focusing on the winter survival of subadults it was shown that males were more vulnerable to various mortality factors. First, males were more susceptible to low winter temperatures than females (Gunnarsson 1987b). In a field experiment, the cold-induced component of winter mortality was examined. Male survival (48%) was significantly lower than female survival (81%). This was supported by a significant correlation between change in the proportion of males in the study population and mean temperature in February (Gunnarsson 1987b); the lower the temperature, the higher the reduction in proportion of males in the population. Second, in a laboratory experiment at low temperatures, males increased their activity significantly when the ambient temperature was raised from +5 °C to +10 °C (Gunnarsson 1987b). Females did not respond to such a temperature increase. Consequently, males became more active during warm winter days, which occurs frequently during winter in SW Sweden, and thereby expose themselves to hunting passerines. Third, in a 2-year field experiment the selective predation by birds on male and female *P. phrygianus* was studied in southern Scandinavia (Gunnarsson 1998). In one of the winters investigated, the predation pressure by birds on male spiders was stronger than on females. Males were affected by a predation pressure that was approximately twice that on females. As a result, the population sex ratio in spring differed significantly between branches protected from bird predation and control branches. On net-enclosed branches there were 34% males vs. 13% males on control branches. The normal sex ratio in Swedish forests is ca. 33% males (Gunnarsson 1987b, 1989) and this also applies to the primary sex ratio (Gunnarsson & Andersson 1992). In the other winter studied, the sex ratio did not differ significantly from the primary sex ratio (Gunnarsson 1998).

In a field experimental study, the survival of the sexes of two lycosid spiders, *Hogna helluo* and *Pardosa milvina*, was compared (Walker & Rypstra 2003). Researchers tested the hypothesis that there is a correlation between life-style and mortality, as suggested by Vollrath & Parker (1992). The two lycosids examined differed in their sexual size dimorphism and activity but they occurred in similar habitats (soybean fields in the present case). The experimental design of the study included an estimation of sex-specific survival in aluminium flashing exclosures with known numbers of individuals added. However, all the exclosures had open tops, so both invertebrate and bird predators could attack spiders during the entire study (1 or 2 weeks depending on species). Walker & Rypstra (2003) found significant differences in *Pardosa*, where males suffered from a higher mortality than females, but not in *Hogna* survival. The result was, however, not in agreement with the Vollrath-Parker (1992) hypothesis because *Hogna*, but not *Pardosa*, showed a significant difference in activity so that males moved longer distances than females. It is also possible that bird predation mainly acts on *Pardosa* because they are day-active but *Hogna* is a nocturnal species (Walker & Rypstra 2003). Why there was a survival difference between the sexes of *Pardosa* in this study remained unexplained.

The maintenance of color polymorphism is often attributed to frequency-dependent preda-

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tion. For instance, the common color morph will be eaten disproportionately often by visual predators and this will maintain a polymorphism in the population (e.g., Allen 1988). In certain spiders, color polymorphism has been described and different types of balancing selection have been shown to be involved in the maintenance of the color morphs (Oxford & Gillespie 1998). It has also been suggested that there are female-biased color polymorphisms in spiders that could be maintained by differential bird predation (Stamps & Gon 1983). However, no data have been presented to support this hypothesis. Only a few studies have attempted to test the importance of bird predation on color variation in spiders. Studies on the Hawaiian happy-face spider *Theridion grallator* showed that balancing selection affected the color morph frequencies and apostatic selection by bird predators was offered as an explanation (Gillespie & Oxford 1998). However, no actual tests were performed, although moving individuals of *T. grallator* were caught during one year. Few individuals (18) were trapped in sticky coating on the underside of leaves. Five individuals were immatures and the rest were adult males. Possibly, this suggests that males are more vulnerable to bird predation because their frequent movements puts males at higher risk for detection (Avery & Krebs 1984).

In *Pityohyphantes phrygianus* there is continuous variation from pale to dark color, probably caused by polygenic inheritance (Gunnarsson 1987a). Melanic individuals were shown to be more active at low temperatures than individuals with paler coloration. This suggested that melanics should be more vulnerable to bird predation during winter when some activity by *P. phrygianus* occurs on suitable days with temperatures between 4 and 10 °C (Gunnarsson 1985). Data from a large field experiment (Gunnarsson 1996) with spruce branches protected from bird predation were used to evaluate this hypothesis (Gunnarsson 1993). However, no support for differential survival of color morph was found in this experiment. It should be noted that melanics usually only make up between 3% to 4% (range 1% to 8%) in the natural population (Gunnarsson 1987a) which makes it difficult to establish significant changes in the population due to sampling error.

Selection on behavior and species composition.—The risk of a spider being eaten by a bird may depend on the individual's behavior. Important aspects of the behavior of spiders are often related to the species, genus, or family. Hunting strategies, for instance, divide families into web-building and free-hunting, or cursorial, spiders. Web-builders could further be divided into several sub-groups depending on web architecture. Blackledge et al. (2003) suggested that predators, mainly sphecid wasps, have been important selective forces for the evolution of three-dimensional webs as a defense against such predation. So, if visually hunting predators exercise a strong selective pressure on spiders, there should be many aspects of spider biology that could be attributed to such selection. Indeed, there seems to be evidence for this conclusion. One example could be the vast variation and complexity of anti-predator devices, which have been comprehensively reviewed by Cloudsley-Thompson (1995) for spiders in general and by Edmunds & Edmunds (1986) for West African orb weavers. The studies reviewed below have examined the effects of bird predation on differences in behavior, including selective predation on the various families, in experimental investigations.

Avery & Krebs (1984) showed in aviary experiments that active spiders were at higher risk of being eaten by Great Tits (*Parus major*) than sedentary spiders. Individuals of *Zygiella x-notata* (Clerck 1757) were released at each of 15 points in the test cage. Trials lasted for 10 min and tests were performed at 2–13.5 °C. Previously, spider activity had been measured at 2–20 °C. There was a good agreement between bird capture rate and spider activity. At low temperatures (2–7 °C) spider activity was low and few spiders were captured. However, both capture rate and spider activity increased rapidly when temperature increased from 7 to 9–10 °C. Above 10 °C, there were only minor increases in capture rate and activity.

In a study of *Agelenopsis aperta*, Riechert & Hedrick (1990) examined anti-predator behavior in two populations (see details above, ''Bird predation on single species''). They found that individuals that were experimentally disturbed in their webs reacted differently in the two populations. Grassland spiders that experienced low bird predation pressure returned significantly faster to their funnel entrances after disturbance than did spiders at the riparian site. The bird predation pressure was

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strong in the riparian habitat (see above). This difference in anti-predator behavior was also found in second-generation laboratory-reared individuals. This is strong evidence that birds can affect the evolution of behavioral traits in spider populations.

One specific behavior that deserves to be mentioned is the construction of webs. It is possible that birds use webs in the vegetation as an indicator of the presence of spider prey. There are observations in the wild of birds hovering close to webs and capturing spiders (e.g., Edmunds & Edmunds 1986). It has been argued that inclusion of stabilimenta could function as visual advertisement so that predators such as birds could avoid accidentally flying into sticky webs (Eisner & Nowicki 1983). In field experiments, some webs spun during night were artificially marked with white paper cut to resemble an X-shaped stabilimentum. Other webs were left untouched as controls: in both cases the resident spiders were removed. The persistence of webs was then followed during the day. By noon there was a highly significant difference between the web categories. Most of the unmarked controls were destroyed, only 8% were left, whereas $> 60\%$ of the artificially marked webs were still intact. In another experiment, Horton (1980) could show that birds preferred to take *Argiope* spp. outside the web rather than on the web and that spiders on webs without stabilimenta were taken more often than spiders with stabilimenta. However, stabilimenta clearly could have a number of functions such as predator-defense, camouflage, prey attraction, etc. (e.g., Robinson & Robinson 1970; Eberhard 1973; Edmunds 1986; Schoener & Spiller 1992; Blackledge 1998), but this review will not cover aspects on this particular issue.

The hunting behavior of spiders is more or less fixed. This means that spider foraging categories often correspond with genus, or family. Consequently, a way to study the evolution of behavior is to examine families with differences in hunting behavior (see e.g., Shear 1986; Vollrath 1988). Here I summarize two studies on the impact of bird predation on different spider families.

In a field experiment (details given above, see also Gunnarsson 1996), Gunnarsson (1995) examined the relative abundance of certain families on spruce branches that either were net-enclosed (mesh size 10 mm) or controls without nets. Sampling was done in the fall and spring during two years and there was special focus on the overwintering populations. Families Clubionidae, Thomisidae, Linyphiidae represented free-hunting (C, T) and web-building spiders (L), respectively. The relative abundance was used in this study, so changes between families suggest that they were favored, or disfavored, in some way because of bird predation. This does not necessarily suggest that birds directly affect the different spider families in spruce trees because other factors, such as competition, or interspecific spider predation, could be involved. A re-analysis of the three families, plus several other families, using density data based on numbers per branch-mass, showed that free-hunting spiders as Clubionidae, but not Thomisidae, were affected negatively by bird predation (Gunnarsson, unpubl.). Web-builders such as Linyphiidae had a higher relative abundance on control branches. This could be a result of changes in competition between different families and of methodological problems. For instance, low densities of clubionids perhaps facilitated web construction of linyphiids. On the other hand, enclosing branches with net-sacks might have modified the micro-habitat on branches so that web-building was more difficult. The re-analysis of family densities suggested that both free-hunting and web-building families were directly affected by bird predation (Gunnarsson, unpubl.).

In another experiment, insectivorous birds were excluded by means of cages in ponderosa pine (*Pinus ponderosa*) (Mooney & Linhart 2006). The reason for doing the experiment was to examine differences in the strength of trophic cascades in arthropod communities in pine and its parasite, dwarf mistletoe (*Arceuthobium vaginatum*). The experiment continued for three years and arthropods were sampled by visual counting on pine branches and foliage. Seven categories of arthropods were sampled: among them hunting spiders (Salticidae and Anyphaenidae) and web-spinning spiders (Theridiidae) were recognized. The main result was that birds had no effect on growth of pine and mistletoe via predation on predatory arthropods, for example, hunting spiders, and foliage-chewing herbivores that were not tended by ants. The predatory arthropods increased their predation pressure on herbivores that were protected against bird predators. So, the

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predatory arthropods compensated for the loss of bird predation. However, pine growth was significantly reduced when birds were hindered from feeding upon aphids. This occurred only if tending ants were present because they protected the ants against arthropod predators. This produced a linear food chain from birds via sap-feeding aphids to pine, whereas the reticulate food web involving predatory arthropods (including hunting spiders) and herbivores other than aphids did not produce a trophic cascade. The hunting spiders (Salticidae and Anyphaenidae) were part of the linear food chain and they were significantly affected by bird predation. However, the abundance of web-builders (Theridiidae) did not respond to removal of bird predators.

Similar results were obtained in successive experiments (Mooney 2006, 2007). Abundances of hunting spiders were affected negatively by bird predation but web-spinning spiders were not (Mooney 2007). The presence of ants affected the study system and the interactions between spiders and ants were sometimes stronger than interactions between spiders and birds (Mooney 2006).

DISCUSSION

What general conclusions about bird predation on spiders can be drawn from the present data? Lawton (1999) was rather pessimistic about the possibility to formulate conclusions in ecology in the form of "general laws." This is especially problematic in community ecology where many species interact, making attempts to generalize about ecological processes more or less impossible. It means that contradictory results could be expected when reviewing community ecology work and that site-specific environmental conditions as well as seasonal variations can have large influences on ecological processes. The literature about bird predation on spiders is mainly within "community ecology."

There is no reason to expect that bird predation on spiders is an important ecological process in all combinations of time and space. Nevertheless, the data collected in this review showed that birds generally are important predators on spiders in forest habitats whereas effects in open ecosystems, such as grassland, were not well investigated. Canopy-living spiders were especially affected by birds, but ground-living species did not show any strong response to bird predation. Part of the reason why ground-living spiders did not seem to be strongly influenced by birds could be that few investigations have tested this hypothesis. However, field experiments have shown that predation by birds can depress other arthropod populations in grasslands (Joern 1986; Bock et al. 1992). For instance, the density of adult grasshoppers in plots with exclosures was > 2.2 times the density in control plots and for nymphs the effect was even stronger (Bock et al. 1992).

Table 2.—Bird predation effects on arthropod taxa in field experiments. Effects are given as mean percentage difference in density between exclosures and controls. Only statistically significant differences are included. Data taken from Holmes et al. (1979), Gunnarsson & Hake (1999), Evelegh et al. (2001), Van Bael et al. (2003), Recher & Majer (2006), and Mooney (2006, 2007).

Taxon	Mean percentage difference	*n*	Range
Dermaptera	2687	1	–
Opiliones	1248	1	–
Heteroptera	593	1	–
Neuroptera	450	1	–
Lepidoptera	398	4	43–1200
Psocoptera	393	2	207–578
Coleoptera	254	2	76–432
Blattodea	201	2	98–304
Homoptera	195	2	103–287
Araneae	194	4	92–390
Hymenoptera	106	2	79–133
Diptera	58	1	–

Insectivorous birds may perform "ecological services" by eating pests but they also consume a lot of predatory arthropods that could be regarded as beneficial to humans. It is even possible that birds prefer certain arthropods, such as spiders, because they have high nutritious value and they do not, as far as we know, emit defensive chemicals that might be toxic or unpleasant to vertebrate predators. If spiders were preferred over herbivorous insects, the "ecological service" done by birds could be reduced.

A tentative test of this idea was performed by comparison of data on bird predation effects reported in seven studies. The data used were taken from investigations where density data for many arthropod taxa were given (Table 2). I included only taxa that had a statistically significant response to bird predation and data

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were restricted to arthropods living in tree canopies to make the results from different studies comparable. The difference between arthropod density on foliage protected from bird predation and controls was given as per cent change. Following Van Bael et al. (2003), it was calculated as [(density on protected branches − density on controls) / density on control] × 100. Only one estimate per taxon and study was used, so if many estimates were available for a taxon, an average was calculated. The obtained values indicated how much removal of bird predation changed the density of each taxa. This could be used as an indirect assessment of birds preferences regarding prey. The higher the percentage change, the more that prey was preferred by the birds.

The available data suggested that spiders were not top-ranked among the taxa (Table 2). Thus, using the present data-set, there was no indication that birds prefer spiders to other arthropod prey taxa. However, it should be noted that spiders and lepidopteran larvae were significantly affected in four studies. This suggests that these two common taxa were often affected by bird predation in forest canopy systems. In the other taxa, the effects were shown in one or two studies, suggesting that the response to bird predation was dependent on specific conditions and occasionally the predation pressure lead to reduced prey density. Although the data were biased towards forest ecosystems, there was no strong indication that bird predation on spiders "reduced" the ecological service done by birds on pest insects. There is at least one experimental study that examined the impact of bird predation in combination with spider predation on lepidopteran caterpillars (Hooks et al. 2003). In a *Brassica* agroecosystem, there was significantly higher productivity in plants that were protected by predators. However, birds and spiders together did not reduce caterpillar densities more than did either predator alone. It was also concluded that birds were the most important predators on the caterpillars in the study system (Hooks et al. 2003).

The influence of bird predation on species number and diversity of spiders is still not completely known. In one experiment the number of spider morphospecies increased on *Eucalyptus* saplings protected from bird predation (Evelegh et al. 2001). Results from spider communities in coniferous trees suggest that different guilds and families could show different responses to predation by birds. The relative abundance of large hunting spiders (Clubionidae) increased in the absence of predation in spruce branches (Gunnarsson 1995). Similar results were obtained in pine trees where hunting spiders (Salticidae, Anyphaenidae) were affected negatively by birds whereas web-building species (Theridiidae) were unaffected (Mooney & Linhart 2006). Blackledge et al. (2003) suggested that hunting behavior may influence the risk of being captured by birds. If this hypothesis is correct, then hunting spiders without web and/or retreat should suffer more from predation than web-building spiders. This hypothesis, however, is not yet well tested in predator-prey systems with spiders and birds. It is also possible that the interaction between bird predation and microhabitat structure affects spider species richness (e.g., Gunnarsson et al. 2004). Further field experiments will help to elucidate the relationship between bird predation and spider species richness and diversity.

The impact of vertebrate predation on spider diversity has been examined in tropical archipelago systems with lizards as top predators. In their study, Spiller & Schoener (1998) found that spider species richness declined when lizards were present. In particular, large and rare species were negatively affected by predation whereas the impact on common species with smaller size was not statistically significant. Moreover, the mean body size of *Argiope argentata* (Fabricius 1775), a relatively rare species in the system, was much larger in the exclosures without lizards than in controls. A similar effect could be expected for bird-spider interactions given that the bird predation pressure on large spiders is higher than on small spiders in both community studies (e.g., Gunnarsson 1996) and single species studies (Gunnarsson 1998; Gruner 2005). Consequently, it could be predicted that intensive bird predation on spider communities will lead to low species richness and large-sized species should be the most vulnerable. This could lead to a trophic cascade if the birds and spiders are part of a linear food chain (Mooney & Linhart 2006). Again, only well designed field experiments will help to examine this hypothesis.

The abundance of ants in tree-canopy systems can influence the bird-spider interaction because ants are competitors to both

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spiders and birds. In a boreal forest in northern Scandinavia, Haemig (1992) found that birds spent more time foraging in trees where ants had been experimentally removed than in trees with ants present. Moreover, insects and spiders had higher biomass in trees without ants (Haemig 1994). This means that birds and ants in spruce and birch trees of boreal forests may compete for a common resource, i.e., other arthropods. However, ants may also interact with spiders. In an experimental study in Oregon, Halaj et al. (1997) showed that competition can occur between canopy-living ants and spiders in Douglas-fir (*Pseudotsuga menziesii*). Although the abundance of hunting spiders (mostly Salticidae) increased significantly in trees without ants, web-building spiders (e.g., Theridiidae, Araneidae, Linyphiidae) did not respond numerically to ant removal. Interference competition was the most likely explanation for the variation in hunting spider density between treatments because ants included spiders in their diet to a low extent only (≈1% of the prey). These results indicated that future studies of bird-spider interactions should include ant density as a ''covariate'' in the analysis of spider abundance. Mooney (2006, 2007) has recently shown that spider - ant interactions can influence bird predation effects on spider populations. The relationship between bird predation and spider abundance may not be as straightforward as generally assumed in earlier studies.

The demonstration of bird predation as a potentially important selective force on spiders and other arthropods in forest ecosystems leads to several important conclusions. Holmes (1990) pointed out that birds are important and significant selective forces on forest arthropods. The evolution of anti-predator traits that many spiders show (e.g., crypsis and escape behaviors), should be strongly influenced by bird predation in forest ecosystems. This hypothesis is not well examined in field experiments except for a few studies on coloration (see review by Oxford & Gillespie 1998) and anti-predator behavior in *Agelenopsis aperta* (Riechert & Hedrick 1990). The study of *A. aperta* is an example of direct effects of bird predation in combination with trait-mediated effects via changes in behavior. There are probably many important indirect trait-mediated effects that affect spider populations (see Werner & Peacor (2003) for a review on trait-mediated effects). This needs to be examined in future studies. Moreover, the hypothesis that three-dimensional webs protect araneoid sheet weavers from wasps but that birds are of minor importance as selective agents (Blackledge et al. 2003) should be tested experimentally. It is important that several types of ecosystems are included in such experiments because the data presented in the present review show that bird predation pressure is strong in forest systems whereas the importance in open habitats is not yet sufficiently well known.

Another hypothesis that has received much interest in recent years is the evolution of sexual size dimorphism in spiders. The model by Vollrath & Parker (1992) assumes that small, roving males in web-building species have a significantly higher mortality than large, sedentary females. Body size was assumed to be a target to selection in this model. Some credence to this assumption was given by a field experiment to examine winter survival of *Pityohyphantes phrygianus* as males survived at lower rates during one of two winters (Gunnarsson 1998). On the other hand, selection acted against large size in both sexes when subjected to bird predation. It should be noted that in linyphiids the males are large and sometimes larger than females.

Male survival rate in the field was not correlated with body size in the lycosid *Hygrolycosa rubrofasciata* (Ohlert 1865) but males that showed high drumming rates while courting females survived better than males with lower drumming rates (Kotiaho et al. 1999). Foellmer & Fairbairn (2005) found no evidence for the hypothesis that small male size should be selected for during mate search. On the contrary, large males were most successful in one of two populations of *Argiope aurantia* Lucas 1833 studied. Furthermore, in the nephilid spider *Nephila plumipes* (Latreille 1804) male survival was very low (34%) during the search for females and there was no correlation between male mortality and body size (Kasumovic et al. 2007). In these three studies, there were no indications of what predators caused the mortality.

Another problem might be that hypotheses regarding the evolution of sexual size dimorphism have been tested in systems with ongoing reproduction. The selective forces outside the mating season have generally been neglected although the evidence suggests that predation

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pressure from birds is very strong during winter, at least in temperate coniferous forest (e.g., Askenmo et al. 1977; Jansson & von Brömssen 1981; Gunnarsson 1983, 1996). This is potentially important because the sexes may respond differently to environmental conditions, such as food availability, outside the mating season (Gunnarsson & Johnsson 1990). More studies are needed to elucidate the role of bird predation as a sex-selective force during mating season but also during other seasons.

The lack of details regarding selective agents in many recent selection studies calls for new field experiments. In the light of the present review, bird predation is a highly probable selection pressure on spiders in many contrasting forest ecosystems. A combination of several types of studies – descriptive, laboratory and field experiments – will lead us forward in better understanding the ecological mechanisms involved in interactions between birds and spiders and it will also tell us something about the evolutionary consequences on spider populations.

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