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Peregrine Falcon (*Falco peregrinus*) may affect local demographic trends of wetland bird prey species

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The demographic value of existing habitat can be affected by changes in predator populations. In Finland, wader populations increased when the Peregrine Falcon (*Falco peregrinus*) declined, due to poisoning by agricultural chemicals during the 1960–1970. Following regulation of DDT usage, nesting Peregrine numbers have increased more than tenfold, while wader populations concurrently declined. The "protection" hypothesis states that although top predators may negatively affect populations of primary prey species, they may benefit other species populations by suppressing activities of mesopredators, such as egg and chick predation. We studied diet preferences of Peregrine Falcons in south-west Finnish Lapland during a period of falcon population growth, based on indices of species consumption versus availability. Preferred and optimal sized prey species, excluding ducks, were equally abundant on bogs with and without Peregrines, and neither did the abundance of non-preferred or non-optimal sized birds differ between bogs with and without Peregrines. Thus, the protection hypothesis was supported for ducks. We found that preferred prey species significantly declined in numbers over time, while populations of non-preferred and non-optimal sized prey species declined less or remained stable, as expected if Peregrines would have direct negative effects on prey species. However, local effects were apparent when comparing local versus national trends of suitable and less suitable sized prey for the Peregrines. While the raptors' role in the population declines of wetland species must have increased after their recovery in the 1970s, this effect might be difficult to separate from other concurrent effects of habitat loss.

1. Introduction

Predation is a strong interaction in animal communities that can affect prey population sizes (Krebs *et al.* 2004). Whether predation has consequences on a prey population depends on the ratio between prey and predator numbers and the importance of the prey species in the predator's diet (e.g., Korpimäki *et al.* 1991). The simplest way of evaluating prey importance for a given predator is by estimating proportions of prey species in a predator's diet. Central place foragers i.e., animals that rear their young in a fixed place, must find food within a limited area, in contrast to free-moving, non-nesting foragers, which are not bound to any specific site within a home range. Raptors that specialize on birds generally have relatively low prey densities around their nests, which may be further depleted during the breeding season (Norrdahl & Korpimäki 1998, Forsman *et al.* 2001). Such declines in prey density may be due to direct predation or because prey species relocate to avoid predators' hunting ranges (Norrdahl & Korpimäki 1998). Breeding Pied Flycatchers (*Ficedula hypoleuca*) for instance, showed a unimodal distribution pattern around nests of the Sparrowhawk (*Accipiter nisus*) with densities peaking at 400 m from Sparrowhawks' nests, suggesting such avoidance (Thomson *et al.* 2006).

Conversely, species that are only weakly predated by a specific predator, or not at all, may benefit from a protecting "umbrella effect", provided against other conspecific predators and mesopredators, such as Hooded Crows (*Corvus corone*) or small mammals. This may substantially lower the predation risk for such unselected species, and could thereby enhance local productivity and population size (Wiklund 1982, Suhonen *et al.* 1994, Norrdahl *et al.* 1995, Blanco & Tella 1997, Mönkkönen *et al.* 2007, Quinn & Ueta 2008).

Many wader species have declined dramatically during the last decades, both in Finland (Valkama *et al.* 2011) and globally (e.g., Amano *et al.* 2010, Thomas *et al.* 2006). Habitat degradation/loss on wintering and breeding grounds,e.g., due to draining and changes in agriculture, has been suggested as the main cause for these declines (e.g., Wilson *et al.* 2005, Thomas *et al.* 2006, Amano *et al.* 2010, Rakhemberdiev *et al.* 2011). More generally, population declines are a consequence of increased mortality or decreased natality, or both factors acting in concert. For example, the dramatic decline in the Temminck's Stint (*Calidris temminckii*) population in the Bothnian Bay in Northern Finland was mainly caused by increased adult and juvenile mortality, probably occurring over a wide geographical range (Koivula *et al.* 2008). Increased nest losses due to ground and avian predators have also decreased reproductive success and thus recruitment rates, contributing to population decline (Valkama 1999, Rönkä *et al.* 2006, MacDonald *et al.* 2008, Teunissen *et al.* 2008). General declines in wader populations coincide roughly with the demographic recovery of the Peregrine Falcon (*Falco peregrinus*; hereafter Peregrine) after this species' global demographic collapse in the 1960–70s due to mass use of agricultural pesticides (e.g., Newton *et al.* 1989, Ratcliffe 1993).

The Peregrine is an important predator of many waders, ducks and gulls in Northern Fennoscandia (e.g., Sulkava 1968). As it mainly hunts flying birds (Ratcliffe 1993), its predation during the breeding season seems to focus on adult birds that are drivers of wader population demography (e.g. Koivula *et al.* 2008), as opposed to eggs and chicks. The increase in Peregrine breeding numbers in Northern Fennoscandia starting in the 1990s (Rauhala *et al.* 2015) makes plausible that there is a direct relationship between predator and prey populations. Since not all populations of species breeding in wetland habitats have declined – some have remained stable or even increased (see Rauhala 2009, Rajasärkkä 2011, Valkama *et al.* 2011) – we have the opportunity to examine the extent to which the protection hypothesis can explain population patterns.

This study was conducted during the period of increasing Peregrine abundances. Numbers of wetland birds, i.e., birds living in open fens and in their edges, have been recorded for many decades in the municipalities of Simo and Kuivaniemi, in southwest Lapland, 50–100 km east of the Bothnian Bay in Finland (Rauhala 2009, Rauhala *et al.* 2001). Peregrines have long nested in the area, but in 1970, when entire Finnish population numbered about 30 pairs (Ollila 2014), this area was occupied by only 1 or 2 pairs. By 2006, 7–8 nesting pairs of peregrines were recorded annually among 8–11 territories (Rauhala *et al.* 2015). By utilizing a combination of collections of remains from these Peregrine nest sites, and wetland bird census data from Simo and Kuivaniemi for 15 selected species, we first aimed to quantify by diet composition analysis (Aebischer *et al.* 1993) whether Peregrines prefer certain prey species and avoid others and what might explain such patterns. To our knowledge, there are only two detailed studies of Peregrine's breeding season prey choices (Hunter *et al.* 1989, Rauhala *et al.* 2001), with the study by Rauhala *et al.* (2001) conducted in Simo and Kuivaniemi.

Secondly, we analyzed whether Peregrine presence or absence relates to wetland bird numbers by comparing communities in fens with and without Peregrines. We predicted that prey species preferred by Peregrines would be less abundant in sites where falcons breed than where they did not. Conversely, less preferred and non-prey species may be more abundant in Peregrine fens if they benefit from the Peregrines acting as deterrents to generalist mesopredators. Finally, we tested for relationships between Peregrine diet preferences and potential prey species populations at broader spatial scales, by comparing local versus country-wide population trends of preferred and avoided species. We assume that our surveyed areas experience a greater Peregrine impact than the country as a whole (see discussion). Under the "protection" hypothesis, we thus expect more negative local than national population trends for preferred species than for less preferred species, and stronger effects in local areas of higher versus lower Peregrine densities.

2. Material and methods

2.1. Study area

We studied Peregrine nests and counted birds primarily in fen areas of the municipality of Simo, in southwest Lapland, Northern Finland (Rauhala 2009), which cover 76,560 ha, 54% of Simo's total area. The habitat includes bogs with numerous small ponds and small lakes, which are used as breeding habitats by waterfowl [mainly Teals (*Anas crecca*), Mallards (*A. platyrhynchos*) and Pintails (*A. acuta*)], diving ducks [Goldeneye (*Bucephala clangula*), Tufted Duck (*Aythya fulicula*), Common Scoter (*Melanitta fusca*), Smew (*Mergus albellus*)] and divers [Black-thorated Loon, (*Gavia arctica*), Red-throated Loon (*G. stellata*), Horned Grebe (*Podiceps auritus*)]. Smaller and shallower ponds are used by small waders and gulls. Larger waders like Curlews (*Numenius arquata*), Whimbrels (*Numenius phaeopus*), Golden Plovers (*Pluvialis apricaria*) and Lapwings (*Vanellus vanalleus*) favor dryer parts of the bogs. A large portion of the woody bogs has been dried for timber production and some of the open bogs for turf production.

2.2. Collection of prey remains

Prey remains were collected by V-M K at 11 breeding sites of Peregrines in Simo between 1992–2009 (Supplementary file 1), mainly in the nest cup and close vicinity of the nest. At some breeding sites, sample collection occurred more than once per season; we pooled all collections from each site to provide more robust samples of prey specimens. The 53 samples available included both fresh (1,073) and old (478) specimens of identified prey, with 1–10 (average of 4.8) samples and 3–51 fresh and 3–87 total specimens per territory. We pooled old and fresh samples to increase sample sizes and thus the number of cases for the preference analyses. While samples of old specimens may be biased towards larger prey specimens, which preserve better in the breeding sites (Sulkava 1968), there appeared to be no large bias in our data, as only Teal and Black-headed Gulls (*Larus ridibundus*) were more numerous in the older samples (Supplement 1). Identification of bones and feathers was completed using the reference collection at the Zoological Museum, University of Oulu. The three largest *Anas* species: Mallard, Pintail and Wigeon (*A. penelope*), were pooled as "large Anas" because of their similar bone shapes and overlaps in size.

2.3. Bird counts

Bird counts were completed by PR during 1982–2009 in 14 fens, using the line transect method for waders and passerine birds. Birds were counted in a 50 m wide main belt, and also outside the main belt in a supplementary belt to form an overall "study belt" (Järvinen & Väisänen 1975). Transect lengths varied from 1.5–7 km, usually arranged as a polygon, but sometimes approaching a straight line, depending on the structure of the bog and the route needed to avoid double counts of birds. If more than one count was done in the same bog in the same year, the count results and transect lengths were summed. In all, our data represent 245 km of transect data. In bogs where Peregrines were nesting, most transects passed within 500 m of the nest, which were usually situated in the best wader fens on dryer ridges, "strings" formed of moss and turf located between the wet areas.

We used bird density (pairs / km^2) for compositional analysis, which considers all observations in the study belt utilizing correction coefficients for land birds taking into account their different detectability (Järvinen & Väisänen 1983). Waterfowl and gulls densities were estimated by total counts for each fen, since the line transect method is not suitable for these groups (Koskimies & Väisänen 1988). However, since waterfowl densities were not available for all fens, we also used the index "species individuals observed / km walked ('frequency')" as an additional measure of each species' abundance estimates for trend analyses.

We utilized national wetland bird census data from Metsähallitus (the agency responsible for administration of Finland's forests), Fisheries and Game Research Institute and the Natural History Museum of Helsinki University (Rajasärkkä 2011, Hario & Rintala 2010, Lehikoinen *et al.* 2012) to compare regional trends with our local data. Since data were often presented as percentage rates for population change, while we calculated regression coefficients, we standardized both metrics to allow a comparison.

2.4. Calculating prey availability per nest site

Bird counts and collection of prey remains were seldom carried out in the same year. We therefore weighted count data spatially and temporally in relation to prey data. Peregrines are capable of hunting in large distances around their nests. For example, in North America, 60% of hunting locations were within an 8 km radius from the nest, but 20% of hunting sites were recorded beyond 23 km maximum mean flight distance in 56 hunting trips for males and females being about 13 km (Enderson & Graig 1997). In the Kola Peninsula, Russia four radio tagged breeding females hunted over an area covering 1,175 km^2, on average, with their hunting ranges overlapping (Ganusevich *et al.* 2004). Given these observations, we assumed that falcons hunt regularly within 10 km of the nest. Thus, we considered counts closer than 10 km as such, but weighted counts further than 10 km from the nesting site with the simple formula:

$$C_d = \frac{1}{d_{ij}} \tag{1}$$

where, d_{ij} is distance of i^{th} transect line to j^{th} nesting site.

To apply a temporal adjustment we weighted each count of a focal species by a temporal distance:

$$C_t = \frac{1}{|t_i - t_{j\pm y}|} \tag{2}$$

where, t_i is the year of prey collection in the nesting site *i* and $t_{j\pm y}$ is the year of counting of a transect *j* and *y* denotes the temporal distance between the prey collection and the transect count. If *y* was 1 year, weighting factor was assessed 1.

The final availability *N* of prey *k* for a specific nesting site *j* counted of *m* transect lines with number of prey *n* in each:

$$N_{kj} = \frac{\sum_{i=1}^{m}(C_d + C_t)}{\sum(\frac{1}{d_{ij}} + \frac{1}{t_{ij}})} \times \mathrm{n}_{ij} \tag{3}$$

2.5. Statistical analysis

We used compositional analysis (Aebischer *et al.* 1993) to assess preference ranks for those prey species identified from prey remains in boggy habitats and for where we had count data. The analysis compares the proportions of prey species in the diet (used) and those in the field (available). We report and analyzed ranked preferences per species, with higher numbers indicating greater usage relative to availability. For availability, we used both the density (species / km^2) and the frequency (species / km^2) as estimates (see above). We had to select informative prey species for the analysis because not all prey species found in remains were found in counts and vice versa. Some species found only infrequently in the remains, e.g., passerine birds were also excluded from the analysis. Proportions for selected species were derived from the totals of all selected species, rather than totals from all species found in the prey remains. Ideally each pair, used versus available, should be proportions of prey species from one nesting site as well as the corresponding proportional availability. However, since our data included only 11 different territories, but with sufficient remains (i.e., > 10 prey specimens) found in only 9 territories, and the number of analysed species should be one less than the number of "used-available" pairs (i.e., territories), only 8 prey species would be able to be ranked for Peregrine preference following this procedure. To allow a broader analysis, we therefore used each prey collection sample, instead of a territory, as a single data point. On average, 4.8 prey samples were collected per Peregrine territory. This could introduce some pseudoreplication (dependency between samples collected in the same Peregrine territories), but we believe this does not present a substantial problem because the long duration of the prey collection study (17 years) would include substantial turnover, thereby decreasing autocorrelation due to bird identity.

To assess temporal trends, and the relationships between Peregrines and wetland species, we formed a series of generalised linear mixed models with negative binomial (family NBI and NBII) error structure by applying the Gamlss statistical package in R (Stasinopoulos, M., http://www.gamlss.org/). Gamlss models are very flexible methods for varying distributions including highly skewed and kurtotic distributions as well as the overdispersion typical of count data (see Stasinopoulos & Rigby 2007). Maximum likelihood was used to estimate model parameters (Bolker 2008). Our covariates were year, to assess temporal trend, and the categorical factor "Falcon Presence", which classified sites as having or not having breeding Peregrines in each year. Peregrines have fixed territories, most of which are annually occupied though not always successful. Counts of each species were related to transect length by an offset function, which scales observations to count effort. Because of the limited sample sizes, we had little power and did not test for potential interactions between year and falcon presence. We compared model fit using Akaike information criteria (AIC), where the lower value indicates a more parsimonious model (Burnham & Anderson 2002). A probability value of 0.05 was used to define a significance level for statistical tests.

In addition to analyses of individual species, we formed 8 categories of species: four taxonomic groups (waterfowl, waders, gulls, passerines) and groupings related to body size and preference. Optimal prey size definition was based the on relationship between size and preference rank of each prey species (15 selected species; note that here we pooled large *Anas* species into one group). Optimal-sized species (12 sp.) were birds that weighed 200–400 g and non-optimal sized birds weighing more or less than that (18 sp.). Results of the compositional analysis were applied to define categories of preferred species (the 8 most preferred) versus non-preferred (the 7 least preferred) prey species.

Finally, we compared trends of each species in our study area to corresponding countrywide estimates obtained from literature (Hario & Rintala 2010, Lehikoinen *et al.* 2012, Rajasärkkä 2011). Our null hypothesis was that population trends should be the same for each species at local and national scales: thus a regression of species trend values between the two scales local vs. regional should be close to 1. Here we also tested whether bird classes preferred, non-preferred and "other birds" had controversial change in local vs. country-wide scale by observing interaction term in linear regression. Significant interaction term would prove for Peregrine-dependence in population changes between these classes.

3. Results

3.1. Diet preference of Peregrine for wetland birds

We had sufficient data to consider preference for the 15 most important prey species (pooling large Anas) in the Peregrines' diet using compositional analysis (see Supplement 1 for the diet). Black-headed and Common gulls, Greenshank, and Teal were the most preferred species, both small and large waders were generally avoided, while Golden plovers, Lapwings, and larger ducks generally had intermediate rank (Fig. 1, Supplement 2). Density and frequency-based measures showed general agreement, with no statistically significant difference between methods (see Fig. 1). Generally, density estimates suggested lower ranks than frequency estimates for waders, except for Curlew and the Whimbrel, the two largest species, while density measures produced higher preference ranks for ducks. The largest differences between two methods of estimating prey availability were found for the Snipe, where density estimation implied 4 ranks lower than frequency esti-

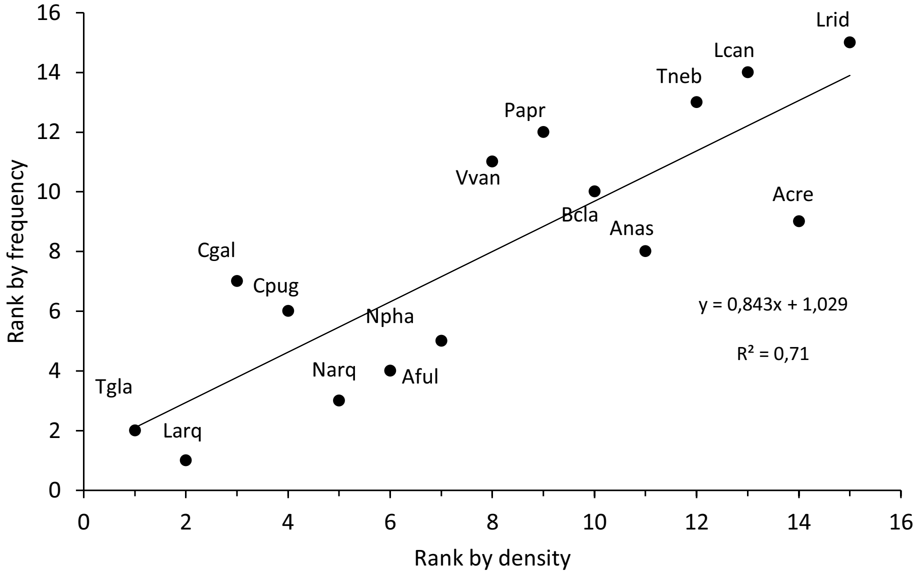

Fig. 1. Peregrine diet preference ranks for 15 wetland species (3 large *Anas* species pooled) calculated using density (pairs / km^2) related to frequency based estimate (birds found / km walked) as availability for the species and simultaneously collected bird prey remain data in Simo bogs during 1993–2009. Explanations for abbreviations of Latin names: Anas = Large *Anas* species pooled, Acre = Teal, Aful = Tufted Duck, Bcla = Goldeneye, Vvan = Lapwing, Papr = Golden Plover, Cgal = Snipe, Narq = Curlew, Npha = Whimbrel, Tgla = Wood Sandpiper, Tneb = Greenshank, Cpug = Ruff, Lrid = Black-headed Gull, Lcan = Common Gull, Larq = Herring Gull.

mation, with the Tufted Duck being the opposite.

When plotting ranks of the 15 prey species against their body weights, a third order polynomial best fit the pattern ($F_{3,11} = 3.558, p = 0.051$) indicating that Peregrines preferred prey weighing around 400 g and tended to use fewer smaller and larger prey than expected by availability (Fig. 2, Supplement 2). Large *Anas* were the most deviant from this pattern, being quite preferred by weighing up to one 1 kg.

3.2. Effect of the Peregrines on wetland bird trends

3.2.1. Local effect: predation vs protection

Ducks were significantly less numerous in bogs where Peregrines were nesting, a trend that was not apparent for waterfowl, waders, gulls and passerine birds (Table 1, Fig. 3). When dividing wetland birds into preferred / non-preferred and optimal sized / non-optimal sized birds, no group was less abundant on bogs with Peregrine nesting sites. The year effect varied among taxonomic groups, being negative and significant only for waders, and among preference classification for preferred and optimal sized species (Table 1), which could be interpreted as a partial support for a negative effect of Peregrines on the wetland birds that they preferred in their diet. Gulls as a group did not decline over the study years, even though highly preferred Black-headed- and Common Gulls declined, since the increase in numbers of Herring Gulls over compensated their losses. For preferred species, population declines seemed to be steeper for species living in Peregrine bogs (Fig 3c), however interactions between Peregrine and non-Peregrine sites were not significant.

3.3.2. Local vs. countrywide effect

We compared local population trends of species ranked for preference against national trends of the same species (see Supplement 3 for data). For this

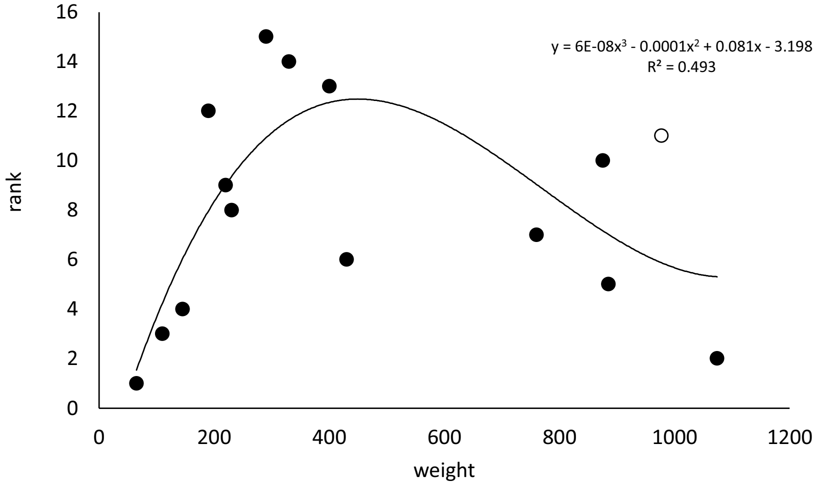

Fig. 2. Peregrine diet preference ranks for 15 wetland species (3 large *Anas* species pooled) breeding in the Simo bog area as a function of body weights. White dot denote large *Anas* species.

analysis, the pooled *Anas* species were split into the 3 original species, assuming similar preference for each species. Rather than a slope of 1, the slope of a regression ($y = 0.280x - 0.035$) significantly deviated from 1 ($t = 3.94$, df = 36, $p < 0.001$) lending support for the Peregrines' negative effect upon its central prey species. The 7 most preferred species showed negative residuals for the line, indicating that species preferred by Peregrines experienced more substantial reductions in abundance than elsewhere in Finland, consistent with, but not proving, a negative impact of Peregrines on their preferred prey. Interestingly, the Ruff (*Calidris pugnax*) and the Lapwing, earlier important (Supplement 1), but now non-preferred prey species of Peregrines (Fig. 1), lay close to the regression line, while the population of similarly important and still preferred prey species, the Black-headed Gull, has collapsed in the Simo bog area. Species that show positive residual values for the line have had more favourable population trends in the Simo area than elsewhere in Finland, consistent with a possible protective influence by Peregrines. Surprisingly, highly preferred Teal, Goldeneye and Golden Plover also belonged to these species, though one would have expected them to be find below the line because of Peregrine hunting in Simo but negligible elsewhere in the country (Fig. 4). Summarizing the message of Fig. 4, we arranged 37 prey species into 3 groups (non-preferred: lower part of preference classification, preferred: upper part of preference classification,

Table 1. Regression coefficients (standard errors) for 8 categories of species between Gamlss-modelled population trends of wetland species in Simo municipality in relation to survey year and the presence (25 counts) or absence of Peregrines (23 counts) per fen. Taxonomic categories are listed. "Preferred" include the 8 most preferred species in Peregrines' diet; and the "Non-preferred" are 7 least preferred. Optimal-sized birds (12 species) weigh 200–400 g and non-optimal size birds (18 sp.) are lighter or heavier than that (Fig. 2). Significant results ($p < 0.05$) are in bold.

Group	Year	*p*	Falcon presence	*p*
Waterfowl	–0.002 (0.018)	0.910	**–0.769 (0.335)**	**0.036**
Waders	**–0.019 (0.008)**	**0.019**	–0.014 (0.143)	0.924
Gulls	0.003 (0.026)	0.918	0.254 (0.658)	0.702
Passerines	–0.007 (0.011)	0.512	0.217 (0.197)	0.276
Preferred	**–0.026 (0.011)**	**0.020**	–0.050 (0.147)	0.803
Non-preferred	–0.001 (0.007)	0.936	–0.005 (0.216)	0.972
Optimal sized	**–0.024 (0.012)**	**0.047**	–0.012 (0.226)	0.958
Non-optimal sized	–0.007 (0.005)	0.184	–0.049 (0.100)	0.630

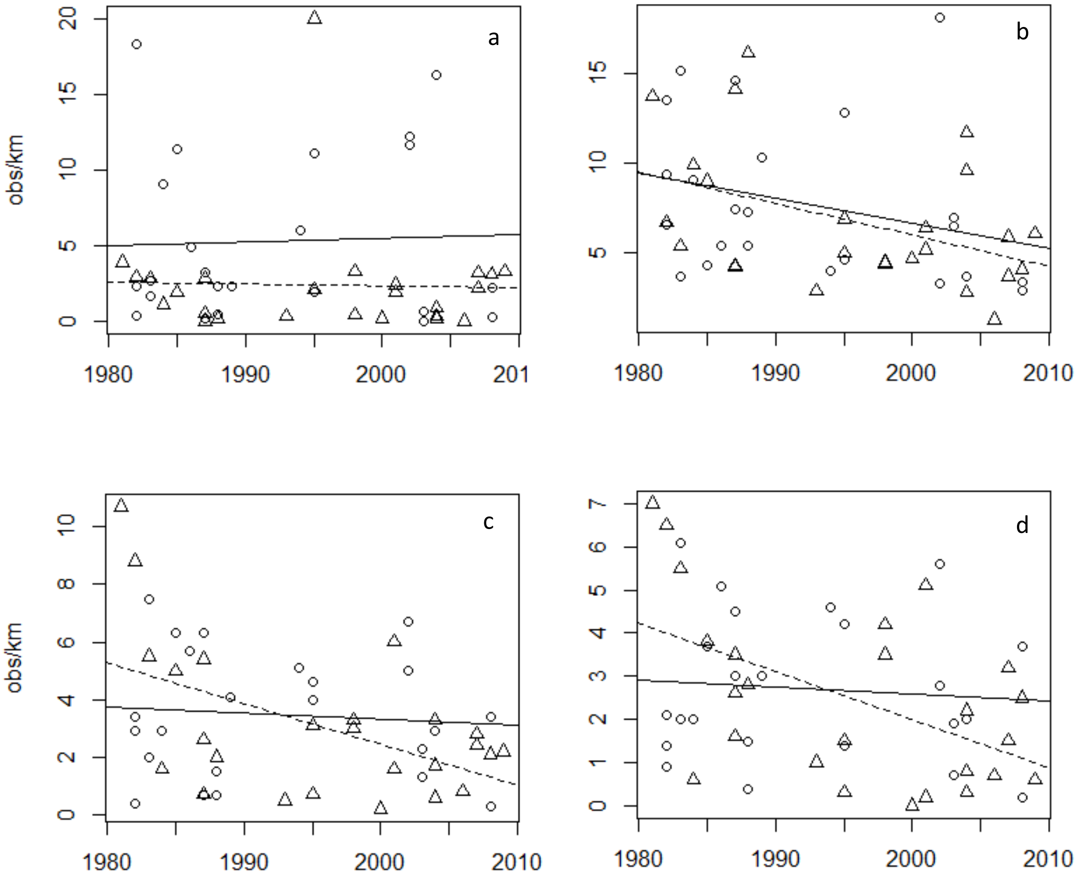

Fig. 3. Population trends of ducks (a), waders (b), preferred (c) and optimal sized (d) species in bog area of Simo in northern Finland in 1981–2009. Regression lines summarize bogs with (dashed) and without (solid) nesting Peregrines.

and others), which shows that preferred species declined more in Simo than elsewhere, but non-preferred prey species have had a slightly more favourable population development in Simo than elsewhere in the country. The interaction term was not far from significance, given our limited power (Estimate = 0.489 ± 0.325, $p = 0.14$), but the whole pattern, however was not significant ($F_{3,70} = 0.944$, $p = 0.424$, Fig. 5).

4. Discussion

4.1. Preference of prey species

Our results suggest that small gulls, Teal and Greenshank are ideal prey for Peregrines, falling within the apparently preferred prey size class of 200–400 g (c.f. Ratcliffe 1993, Van den Hout *et al.* 2008). Using a simple catch/supply ratio as a preference index, Rauhala *et al.* (2001) found a similar preference pattern. It was somewhat surprising to find that Golden Plovers, despite being relatively rare in the bogs, were preferred more than the easily seen Lapwings and Ruffs. Lapwings may be difficult to catch due to their aerial agility (Ratcliffe 1993). Moreover, while male Ruffs are readily visible at lekking sites, they leave the fens soon after the lekking period by mid-June and start their migration (Väisänen & Järvinen 1976, Rauhala, pers. obs.); female Ruffs provide sole care of the broods but are cryptic and thus may not be easy prey for Peregrines. By contrast, both sexes of Golden Plovers care for their brood and because they defend them noisily they are likely to attract hunting falcons (P. Rauhala, pers. comm.,

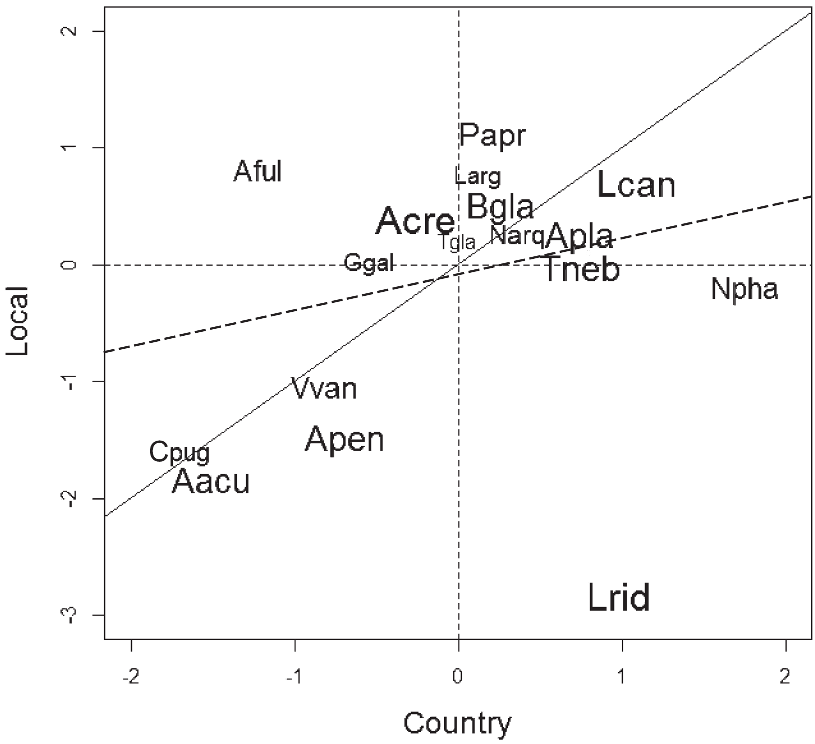

Fig. 4. Comparison of standardised local trends vs countrywide trends for 17 preferred species (Large *Anas* species group were split to three original species each given same rank number as *Anas* sp; 9). Solid line is 1:1 line between standardised local trends and countrywide trends. Dashed line deviating significantly from that represents regression between local and countrywide trends. The size of the species names corresponds to their preference in Peregrines' diet. Find abbreviations of the Latin names in the text for Figure 1 added with Aacu = *A. acuta*, Apen = *A. penelope*, Apla = *A. platyrhynchos*.

Finney *et al.* 2005), which may increase their real availability. It is also possible that numbers of Golden Plovers inhabiting the dryer bog areas are underestimated as surveys concentrated on the so called wet "aapa" fens (Väisänen & Järvinen 1976). Ducks were relatively highly preferred though being rather heavy prey. Their higher weight may make them less agile, and thus comparatively easy prey for hunting Peregrines, and very profitable food items. Hunter *et al.* (1989) recorded the highest preferences by Peregrines for smaller species in Alaska, along the Yukon River, where the preferred species Greater Yellowlegs (*Tringa melanoleuca*) weighed less than 200 g. Apparently, their study reflects the scarcity of larger prey species, since "ideal sized" Teals and mid-sized gulls were hunted by falcons, but neither in such numbers nor were so highly preferred as in our study area.

4.2. Species protection by Peregrines

Most of the Finnish Peregrine pairs, 250–300 at the moment, breed on strings of open and usually watery bogs, which are also the preferred habitats for waders, ducks, and for gull colonies (Rauhala 2009, Ollila 2014, Ponnikas *et al.* 2014). Our findings indicated that ducks avoided Peregrines' presence. Other groups neither avoided nor preferred Peregrines, suggesting some balance between costs and benefits.

Earlier studies of bird communities have shown that densities of suitable-sized prey are lower near the breeding sites of raptors, but neither too large or small prey do not show such density responses or are more numerous near raptor nests than further away (Hunter *et al.* 1989, Suhonen *et al.* 1994, Norrdahl & Korpimäki 1998, Forsman *et al.* 2001, Mönkkönen *et al.* 2007). By killing nest robbing mesopredators, mainly Hooded Crows, Peregrines provide protection for species that are not important as their prey (Paine *et al.* 1990, Norrdahl *et al.* 1995, Quinn & Ueta 2008, Sergio *et al.* 2008). Our data provide only partial support for the protection hypothesis, which states that preferred prey species should avoid the predator, in that preferred duck species avoided Peregrines (Quinn & Ueta 2008).

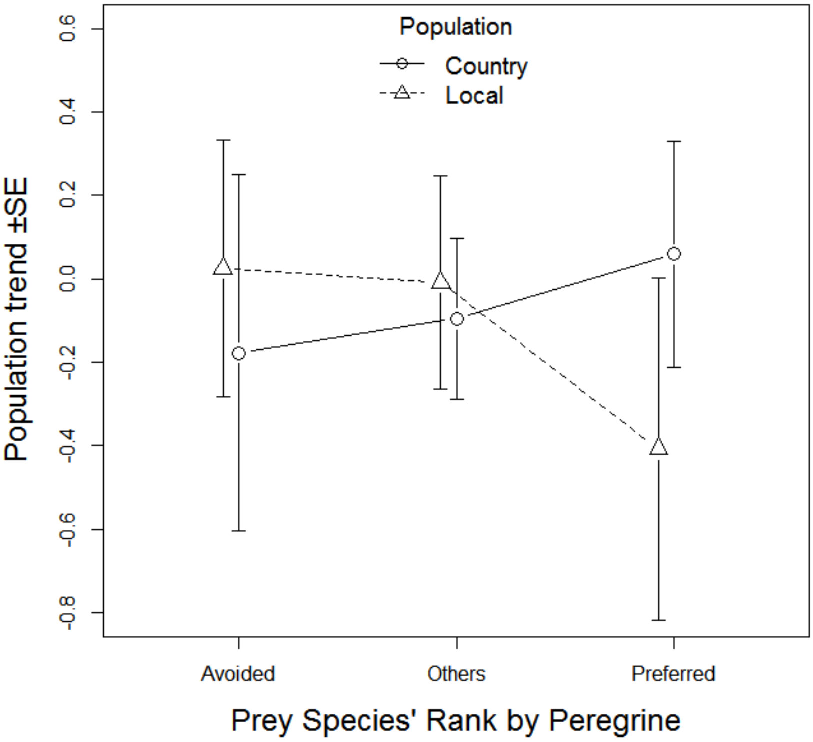

Fig. 5. Comparison of mean local and countrywide trends of wetland species avoided and favoured by Peregrines in their feeding habits. Group "others" denote species found randomly or not at all in the diet. Continuous line with open dots describes countrywide situation while broken line with triangles local situation.

4.3. Peregrine predation on wetland species; local vs country wide effects

Among prey assemblages, populations of waders, preferred- and optimal sized- prey species declined significantly during 1982–2009 in areas with Peregrines, lending support for the a direct negative effect of Peregrines' on their preferred prey species. Comparisons of local with national trends (Fig. 5) seems to support the existence of these local effects (Rajasärkkä 2011, Hario & Rintala 2010, Lehikoinen *et al.* 2012). Intriguingly, the Greenshank, the Common Gull and the Black-headed Gull, among the top five in the Peregrines' preference rank, showed larger negative population trends in the bog areas of Simo than elsewhere in Finland. Rauhala (2004) noticed that the appearance of a nesting Peregrine pair in one side of the large bog of Käärmeaapa strongly affected the densities of nearby Ruffs, Lapwings, Black-headed Gulls and ducks, whose numbers were less affected elsewhere on the other edge of the bog, supporting the idea of birds avoiding Peregrines. Since the main breeding grounds of Peregrines are located in Northern Finland, while most of the gull and half of the land bird and waterfowl monitoring is done in the southern and central parts of Finland (Hario & Rintala 2010, Lehikoinen *et al.* 2012, Rajasärkkä 2011), national bird counts represent, on average, areas of lower Peregrine presence than is the case in our study area (see Sulkava 1968, Ponnikas *et al.* 2014). Therefore, based on correlative evidence the increasing numbers of Peregrines cannot be linked with countrywide declines of Lapwings and Black-headed Gulls, since their distributions only partially overlap with the distributions of the Peregrines.

It is remarkable that wader abundance in the Simo bog area in 2000 was not lower than it was in the 1950s in the same biogeographical area (Järvinen & Sammalisto 1976), which suggests that wader populations flourished when Peregrines were scarce in the 1970–80s. As an example, bird counts in the richest bog of the Simo area, Martimoaapa, show that Lapwings and Black-headed Gulls colonized the area in the 1960s, with densities rising until the 1970s after which they declined, such that in 2000 neither species was observed during surveys (Väisänen & Järvinen 1977, this study). Rauhala's (2009) repeated counts in 10 bogs in the 1980s and in 2000 verify these results. Ruffs may form a more complicated case. According to investigations in western Finland they were absent from the large bogs of Ostrobothnia in the 1950s (Järvinen & Sammalisto 1976), but numerous in the 1970s (Hakala 1971). However, a study of the diet of Peregrine falcons (Sulkava 1968), roughly in the same area during the 1950–60s, found that Ruffs and Lapwings comprised 9.8% and 6.9% of the diet respectively, which was a 4- or 3-fold difference to our data (Supplement 1). The discrepancy between bird counts and percentages are difficult to explain, but it is possible that both species avoided bogs where Peregrines were nesting and inhabited areas that were not surveyed, e.g., littoral areas of the Baltic Sea and lakes.

4.4. Global effects on waders; combination of predation and habitat loss?

The contemporary revival of Peregrine populations (Newton *et al.* 1989) has impacted migration behaviour and body condition of waders (Lank *et al.* 2003, Piersma *et al.* 2003, Ydenberg *et al.* 2003, 2004, Van den Hout *et al.* 2008, Dekker *et al.* 2011). Habitat loss and increased mammalian and avian predation (Koivula & Rönkä 1998, Valkama *et al.* 1999, Wilson *et al.* 2001, MacDonald & Bolton 2008, Teunissen *et al.* 2008) also have contributed to declines in wader populations. Raptors as one mortality factor may have a heavy local impact on waders in their wintering and stopover sites, with losses raising up to 20–50% depending on species and landscape structure (Page & Whitacre 1975, Cresswell & Whitfeld 1994, but see Van den Hout *et al.* 2008).

The increase in numbers of Peregrines and other raptors throughout the breeding areas, migration staging areas and final wintering sites of waders has inevitably raised predation mortality from the period of raptor scarcity in the 1970s (see Piersma *et al.* 2003). Raptor predation likely cannot be the main cause of wader declines, because wader populations are affected in different ways (see Thomas *et al.* 2006). Besides, Peregrine populations have not yet reached the levels that prevailed before the poison catastrophe. Some of the apparent wader declines in breeding and wintering sites may reflect behavioural habitat change rather than population differences, because of altered migration routes and habitat usage, as found for Dunlins and Ruffs (Lank *et al.* 2003, Ydenberg *et al.* 2004, Rakhimberdiev *et al.* 2011). Habitat loss, due to bog drainage for forestry, agriculture and peat production, at breeding sites in Finland has likely had a big impact on wader populations, with roughly 50% of the bog areas in Simo, and across Finland, having been drained (Rauhala 2009). Loss of bog areas began in the 1960s, well before the peak abundances of waders recorded in the 1970–80s. It is possible that the simultaneous disappearance of a substantial mortality factor, raptor predation, masked the effects of habitat loss, or that waders even increased during that time (e.g., Thompson & Thompson 2008). Most monitoring programs started during the 1970s–1980s (Stroud *et al.* 2004), when waders may have been atypically abundant. Therefore, part of the apparent decline in waders may be a return to more typical, lower population densities coincident with the recovery of raptors. At some point, however, sustained habitat loss may have pushed populations below "normal" levels.

Pressure on wader populations has increased because of degradation/loss of habitat and increased predation by mammals, but also by the increase of generalist predators such as Peregrines and other raptors. Since raptors are not dependent on any specific prey species, they may maintain stable populations although populations of specific prey species fluctuate, which can allow a greater relative predation impact as prey populations decline (Ratcliffe 1993, Sinclair & Pech 1996, Tornberg 2001). Recently, Eider (*Somateria mollissima*) populations have declined at least partly as a result of intensified predation of a generalist predator White-tailed Sea Eagle (*Haliaetus albicilla*) on breeding female eiders (Lehikoinen *et al.* 2008, Ekroos *et al.* 2012). Due to habitat loss, waders are now less able to find alternative sites when Peregrines have begun to breed in a fen. Thus, protecting only high quality habitats may in such a case be counterproductive, especially in the conservation of habitat specialists. On the other hand, Peregrines have clearly expanded their diet to take increasingly common species like Woodcocks (*Scolopax rusticola*) and Fieldfares (*Turdus pilaris*) (see Sulkava 1968, Supplement 1), which may provide a buffer against the predation of rarer birds, which may yet benefit from the potential protection given by this superior raptor against nest robbing and chick predation by birds and mammals living on its range. The results of this study suggest that peregrines reduce the abundance of local prey abundance, but additional research is needed to establish whether Peregrines drive population declines.

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Muuttohaukka voi vaikuttaa paikallisesti kosteikkolintujen demografiaan

Kosteikkolintulajien maailmanlaajuisen taantumisen uskotaan johtuvan habitaattien vähenemisestä. Tämän lisäksi näitä lajeja voi uhata myös elpyneet petolintukannat. Kuvaavasti kahlaajakannat kukoistivat 1960–70-luvuilla, jolloin niiden merkittävimmän saalistajan muuttohaukan (*Falco peregerinus*) kannat maailmanlaajuisesti romahtivat ympäristömyrkkyjen seurauksena. Sen jälkeen muuttohaukkakannat ovat elpyneet ja kahlaajakannat taantuneet. Tämän petolinnun vaikutus voi kuitenkin olla monitahoinen. Huippupedot voivat myös suojella petojen kannalta toisarvoisia lajeja pesiä ja poikasia ryöstäviltä pienpedoilta. Huippupetojen suosimien lajien kannattaa sitä vastoin välttää näiden läheisyyttä.

Lounais-Lapissa, Simon kunnassa tekemässämme tutkimuksessa, jossa hyödynnämme tietoa muuttohaukan saalislajien saatavilla olosta ja niiden ravinnon koostumusta havaitsimme, että muuttohaukkojen suosimat n. 400 g painoiset saalislinnut sorsia lukuun ottamatta, eivät kuitenkaan suojeluhypoteesin vastaisesti välttäneet muuttohaukkaa, eivätkä vähemmän suositut ja epäoptimaalisen kokoiset lajit suosineet sitä. Havaitsimme, että muuttohaukan kannalta tärkeät kahlaajat ja pienikokoiset lokit vähenivät enemmän kuin pienet varpuslinnut, tärkeiden sorsalintukantojen säilyessä kuitenkin vakaina. Sama koski suosittuja ja ihanteellisen kokoisia lajeja, taksonomiasta riippumatta, tukien ajatusta muuttohaukan haitallisesta vaikutuksesta sen suosimiin lajeihin. Kuitenkin verrattaessa lajien paikallisia trendejä maanlaajuisiin trendeihin on ilmeistä, että vaikutus on vain paikallinen. Petolintujen merkitystä kahlaajien vähenemisessä niiden toivuttua 1970-luvun aallonpohjasta voi olla vaikeata erottaa samanaikaisesta niin lisääntymis- kuin talvehtimisalueilla tapahtuneesta elinympäristöjen heikkenemisestä.

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Online supplementary material

Supplement 1
Supplement 2
Supplement 3