

# Raptor Habitat Studies – the state of the art

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## ABSTRACT

Research on habitat relationships of raptors and owls has sharply increased during recent decades. I assessed study systems, methods and the main findings in 896 studies that explored hypotheses about raptor-habitat relationships. Ten species accounted for half of the publications and 90% of studies were performed in North America or Europe. Hence, a critical conservation issue is whether, and how, the knowledge can be extrapolated to other situations. Yet only 19% of studies generalized their results beyond target species. Methodologically, there have of late been major developments (growing number of radio-tracking studies, manipulative experiments, measurements of resource abundance, multivariate treatment of habitat characteristics), while other issues remain or have become problematic (independence of observations, yearly pooling of data, some aspects of hypothesis-testing). I summarized findings about varying quality of individual sites and landscapes, preemptive use of habitats, interaction between site and individual quality, and the development of site-quality recognition by birds of prey. Finally, I listed four major gaps of knowledge, the filling of which could significantly enhance both theory and management (sources and patterns of interspecific, geographic and temporal variation in raptor-habitat relationships; adaptivity and trade-offs of habitat selection; concepts of habitat patch and diversity for raptors).

## INTRODUCTION

This paper is a review, compiled for two reasons: (1) even a brief look at recent publications on raptor habitats suggests that most authors have read and use just a tiny part of the relevant studies. Indeed, this could be expected in a situation where there are more than a thousand case studies and only two major reviews (Newton 1976a; Janes 1985), both already published decades ago; (2) reviews and meta-analyses are a powerful tool for detecting random errors and coincidence, given the correlative nature of most bird-habitat studies

(something that will probably never change as experimentation is difficult for most habitat-related problems). Consequently, my aim here is also double. First, I give an overview of the published material, some methodological advancements and problems, questions asked and answered so far. Secondly, I present a more detailed treatment of selected basic problems, which have wide implications for raptor conservation. I also list and discuss major gaps in knowledge, the filling of which could significantly enhance both theoretical understanding and species management. My use of habitat-related terms follows Hall *et al.* (1997). In brief, habitat is an area suitable for an organism to use, habitat preferences are revealed in disproportionate use of environment; and habitat quality refers to the ability of the environment to provide conditions appropriate for individual or population persistence. The latter is in practice measured by some 'shortcut'-variable, here named as 'fitness-correlates' (reproductive success, prey capture rates, physiological condition, energy balance). I use 'reproductive success' as a general term for reproductive indices, although – whenever presented in the original study – I tried to build conclusions on productivity (the number of fledged young per established territory per year; cf. Newton 1979).

## PRINCIPLES OF COMPILING THE REVIEW

I reviewed the literature mostly by searching electronic databases, conference proceedings, national ornithological journals and reference lists. Initially, I considered worldwide all published material up to 2002 (including, although incompletely; Fig. 1), which quantitatively (but not necessarily statistically) explored hypotheses about bird-habitat relationships in raptors and owls (Table 1). I did not consider pure habitat descriptions; therefore, nearly all studies that met the criteria had been published after 1970 (Fig. 1). I also omitted theses, most of which were not readily available and often had their most important results published. According to my list, there are at least 77 PhD dissertations and hundreds of master theses devoted partly or entirely to the subject.

Altogether, I considered 896 studies (70% in peer-reviewed journals). At least 200 additional studies were likely to qualify for inclusion but were unavailable for me. Hence I hope to have covered over three-fourths of the relevant studies in this review. For each publication, I assessed (1) study system – target species, geographic area, spatial and temporal scale, and the generality of conclusions; (2) design and techniques – data-collection approach (observational, experimental, meta-analysis, review), type of hypothesis, field procedures, replication and statistical techniques; (3) the main findings according to some pre-defined subjects. Assessment details as well as a list of references for papers included in this review are available on request from the author.

**Table 1. Treatment of some major habitat-related issues in this paper.**

<i>Treatment</i>	<i>Major issues</i>
Included	Habitat preferences; Habitat quality; Temporal and geographic differences in habitat use; Morpho-physiological correlates of habitat use; Interspecific differences in habitat use; Predictive (HSI) or analytical (habitat-based PVA) habitat-modelling
Included only when explicitly related to habitat characteristics	Comparisons of raptor density or productivity between areas; Limiting factors; Change of nesting or foraging sites; Home-range size; Regularity of nest-spacing; Geographic trends in clutch and brood sizes; Flushing distances to disturbance
Omitted	Raptor diet or prey abundance in different environments; Food-supplementation experiments to influence breeding performance; Raptor density or productivity vs annual variation of prey abundance; Dispersal distance; Behavioural relationships between individuals, which affect spacing patterns

## STUDY SYSTEMS – WIDE-RANGING BUT UNEVENLY REPRESENTED

### Study hypotheses.

Two main types of hypothesis dominated: habitat preferences were in the scope of 557 (62%) and habitat quality in 335 (37%) studies (cf. Table 1). Notably, 350 papers were partly or fully devoted to nesting habitat preferences. Differences between species were explored in 78 and temporal changes in habitat use (seasonal, annual or long-term) in 71 studies, the specific consequences of human disturbance to habitat use were estimated in 63 and habitat availability in 60 papers. In contrast to intensive data-processing, analytical models were rare, and there were only nine attempts (six of these about the Spotted Owl *Strix occidentalis*) of habitat-based population viability analysis. Reports on the individual development of habitat preferences (5 studies) were even less frequent.

### Species coverage.

711 studies (79%) focused on one species, 66 (7%) on two and 35 (4%) on three species, and the remaining 84 studies on more than three species simultaneously. The species coverage was very uneven, with the ten most extensively studied species accounting for half of one-species publications (Spotted Owl – 71, Bald Eagle *Haliaeetus leucocephalus* – 61, Osprey *Pandion haliaetus* – 37, Goshawk *Accipiter gentilis* – 36, Tengmalm's Owl *Aegolius funereus* – 28, Eurasian Kestrel *Falco tinnunculus* – 28, Golden Eagle *Aquila*

*chrysaetos* – 26, Common Buzzard *Buteo buteo* – 24, Peregrine Falcon *Falco peregrinus* – 23, American Kestrel *Falco sparverius* – 22 studies), while 90 species made up the other half. Although many additional species (particularly tropical ones) were represented in the multispecies analyses, probably more than half of the world's birds of prey have not been covered by quantitative studies of their habitat relationships, except perhaps for pure descriptions.

### **Geographic coverage.**

Forty-nine percent of the checked studies had been performed in North America (incl. 43% in the U.S.) and 40% in Europe (incl. 9% in the U.K. and 6% in Spain). The remaining 10% contained 28 studies in Africa, 20 in Asia, 20 in Central or South America and 14 in Australia (and additionally 13 worldwide reviews and 6 studies on raptors in captivity). Although publications from these latter continents were less available for me and a larger share could have been missed, the geographic bias is nevertheless obvious, particularly when the relative species richnesses of these areas are considered.

### **Spatial and temporal scales.**

I distinguished breeding and non-breeding seasons as well as full-year research, and I classified the birds' activities as nesting, foraging, roosting and other (mostly indeterminate) observations. Spatial scales of the processes under exploration were grouped as (1) geographic scale – characteristics of the whole ranges of distinct populations (mostly modelling studies); (2) landscape – habitat of groups of individuals within a population (e.g. comparisons of raptor densities in different environments); (3) home-range (macrohabitat) – long-term area of activity of individuals or pairs (e.g. radio-tracked home-ranges or surrogate circles around nests or other activity centres); (4) microhabitat – sites within home-range.

The frequency distribution of the studies is given in Table 2. The table should be interpreted with some caution, particularly for the home-range scale, since the listed activities reflect the original approach by authors (e.g. whether the home-range in the breeding season represents nesting or foraging). For example, most full-year radio-tracking studies of home ranges yielded "other observations" (not further classified) while the ranges of breeders have been classified as "nesting habitat" (or "foraging habitat" if stated so in the original source). Despite these problems, it is clear that most studies have been carried out in the breeding season, and have focused particularly on nest-site microhabitats. Outside the breeding season, relatively few researchers have tried to distinguish foraging or roosting activities from all observations, particularly at the larger scales. Given that juveniles or immatures of many long-lived raptors have specific 'dispersal habitats', the lack of such studies should also be stressed (the few exceptions are Ferrer & Harte 1997; Miller *et al.* 1997; Ganey *et al.* 1998; Mañosa *et al.* 1998).

Spatial scale of a study may differ from the scale of the process. For example, one may describe microhabitats over the geographic range of a species. Such large-scale patterns of smaller-scale processes are important while extrapolating results from one area to another. For illustrative purposes, I defined geographic study scale as covering at least 200,000 km<sup>2</sup> or areas at



least 500 km apart. Only 10 studies (nine of these about nest-sites) treated raptor microhabitats over such a scale (e.g. Mosher & White 1976; Olsen 1982; Mosher *et al.* 1986; Morris 1993; Shrubb 1993), while none explored home-ranges.

**Table 2. Distribution (numbers) of 891 raptor-habitat studies by season, studied activity and spatial scale. Five additional studies explored habitat-characteristics of whole geographic ranges of raptors.**

Season and activity	<i>Scale of the raptor-habitat relationship</i>			Total*
	Landscape	Home-range	Microhabitat	
<b>Full year**</b>	<b>32</b>	<b>26</b>	<b>134</b>	<b>155</b>
Foraging	4	3	50	52
Roosting	1	1	27	28
Other observations	30	24	70	98
<b>Breeding season</b>	<b>161</b>	<b>176</b>	<b>472</b>	<b>651</b>
Nesting***	156	167	451	610
Foraging	–	7	37	39
Roosting	1	4	14	16
Other observations	14	15	42	57
<b>Non-breeding season</b>	<b>16</b>	<b>9</b>	<b>68</b>	<b>85</b>
Foraging	1	3	16	18
Roosting	–	–	14	14
Other observations	15	7	47	63
<b>Total*</b>	<b>209</b>	<b>211</b>	<b>674</b>	<b>891</b>

\* totals are less than cell sums, since one study may cover more than one activity or scale

\*\* includes three tropical studies for which breeding season could not be distinguished

\*\*\* includes 39 full-year studies, which explored nesting habitat

### Generality of conclusions.

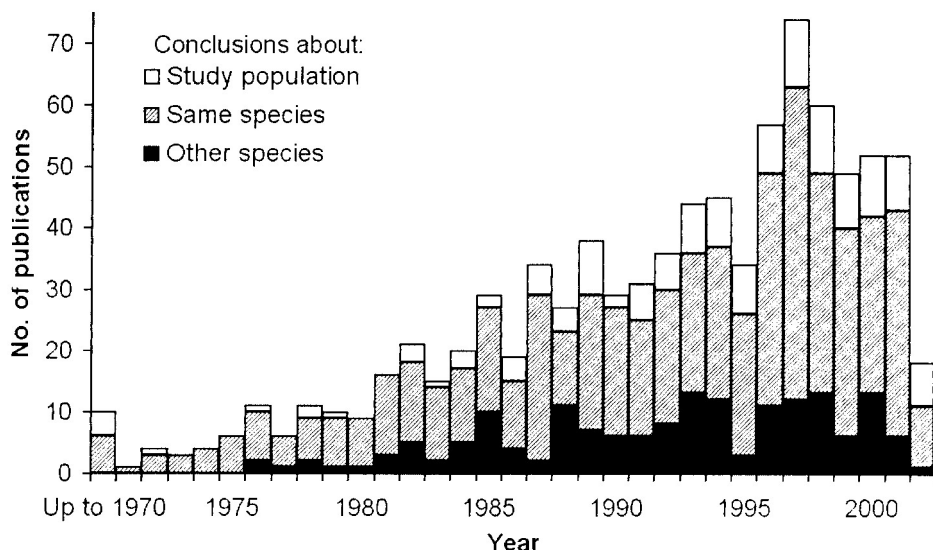
According to my subjective assessment, most studies (64%) viewed their results at (sub)species level, while 19% attempted to generalize the results to other species or communities. In contrast, interpretations in 16% of papers did not go outside the study population. The annual number of papers of general interest has not changed much since the mid-1980s, and the recent increase in publishing is largely due to species-specific research (Fig. 1). Among the 169 studies on the three most extensively studied species, generalizations were relatively rare (7%) and population or methodological approaches were frequent (26%), indicating that the potential of well-studied systems for theory development has been underexploited.

## METHODOLOGICAL ADVANCEMENTS AND TROUBLES

From the methodological viewpoint, there have been some major developments over time in raptor habitat studies (radio-tracking, manipulative experiments, measuring resource abundance, multivariate treatment of habitat characteristics), while other issues remain (independence of observations, yearly pooling of data, power analysis) or have become problematic (multiple tests, stepwise procedures).

**Field methods.** The majority of raptor-habitat studies were (and are still) observational in nature, but at least 60 special manipulative experiments have been performed, and numerous studies have explored raptors' response to anthropogenic changes (e.g., vegetation or landscape change due to forestry or agriculture, burning, military training, recreation, urbanization etc.). The most frequent experiments were those with artificial nests (31), followed by purposeful disturbing (10), artificial perches (5) and patches of supplementary food (5). However, only 27% of manipulative experiments yielded general conclusions (cf. 19% for all studies; Fig. 1). From the other advancements, absolute or relative abundance of prey was measured in at least 73 papers, and radio-tracking was used in 92 studies.

**Figure 1. Distribution of 875 raptor-habitat studies by publishing year and generality of their conclusions. An additional 21 checked studies were either purely methodological or repeated other publications.**



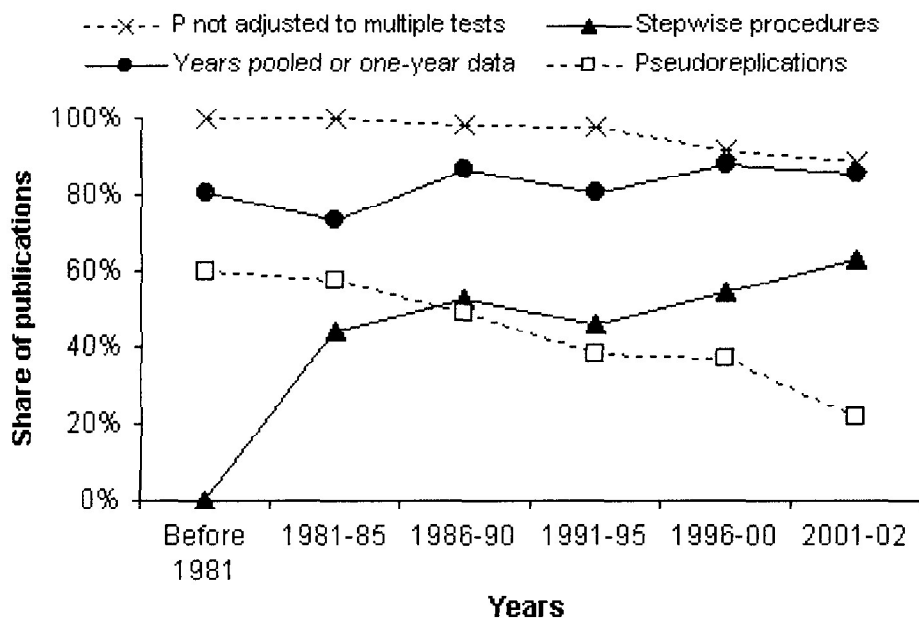
**Non-independence of observations** includes a variety of common methodological errors, some of which are difficult or even impossible to avoid (e.g. at large spatial scales). For instance, I found only three studies that addressed the non-independence of adjacent sites due to spatial autocorrelation (Gibbons *et al.* 1995; Chou & Soret 1996; Bustamante 1997). A better-known error – that repeated measurements of same individuals (pairs, nest-sites etc.) are treated as independent observations – occurred in 42% of 790 studies, but

this problem is being progressively considered (Fig. 2). Finally, 34% of landscape-scale studies ( $n=206$ ) were actually based on one large landscape area (e.g. the urban population of one city versus the rural population surrounding it).

**Treatment of annual differences.** Sixty-seven percent of raptor-habitat studies pooled data from different years and 17% relied on data from only one year. This approach is likely to have concealed important patterns or stressed untypical ones, given that year/habitat interactions have often been found when checked (Löhmus 2003). There has been no improvement during the publishing history (Fig. 2).

**Statistical procedures** of habitat studies are becoming increasingly rigorous. In particular, since Preston (1980), the share of multivariate treatments of habitat characteristics has increased to 45% of all studies in 2001–2002. This, however, has caused a burst of studies using stepwise variable selection procedures (Fig. 2), although these should be used with extreme care if at all (James & McCulloch 1990).

**Figure 2. Changes in the relative frequency of methodological shortcomings among raptor habitat studies. Stepwise procedures were explored among 214 studies using multivariate statistics, and the adjustments of significance levels among 532 studies containing more than five statistical tests. For the other two variables, the sample sizes approach those on Fig. 1. ‘Pseudoreplications’ include only the cases of repeated observations of individuals.**



In the era of extensive hypothesis-testing, one should remember that numerous tests deflate the original significance levels. Yet adjustments to avoid Type I errors (e.g. Sokal & Rohlf 1995) have been made in only 5% of relevant

studies (Fig. 2). Fifty randomly chosen papers (significance levels not adjusted) had on average 26.3 tests per paper, including 9.2 tests significant at  $\alpha=0.05$ . As this number of tests can include on average 1.3 random deviations outside the 95%-probability, 15% of 'significant' tests might have been random errors. Moreover, the share of significant tests was larger in the papers reporting fewer tests ( $r_s=-0.36$ ,  $P<0.01$ ), suggesting that authors tend not to present insignificant tests. Considering also that the papers with negative results are less likely to be published, I suspect that the share of random noise among 'significant' effects is much higher than the estimated 15%.

The absence of an effect may also be an important result if distinguished from non-significant tests due to insufficient power. Yet power tests or related procedures occurred in only eight raptor habitat studies, while necessary sample sizes were estimated in four studies.

Finally, in the light of growing computational complexity, it is striking that 'the paradigm of the mean' still holds, by which I mean that in 94% of statistical analyses habitat descriptions have been reduced to either sample means (e.g. a habitat feature is defined to be preferred if its mean value in sites used by the animal differs from the mean in random sites) or distributions (e.g. contingency tables). Although habitat preference or quality may also be expressed via reduced variance (McCallum & Gehlbach 1988; Clark & Shuter 1999), only 10 papers actually tested variance effects!

## THE FINDINGS

In this section, I summarize the current evidence of four major issues, including two – variations in the quality of home ranges, and the individuals occupying them – which were raised decades ago by Newton (1976a) as subjects for future work.

### 1. Site-dependent population regulation.

To describe how birds of prey distribute themselves in real landscapes, I use the framework of site-dependent population regulation, which includes two main features: (1) environmentally caused heterogeneity among sites (here: territories or home-ranges) in suitability for reproduction and/or survival, and (2) preemptive site occupancy, with the tendency of individuals to move to sites of higher quality as these become available (Rodenhuse *et al.* 1997). Both of these features have been detected in nesting Sparrowhawks *Accipiter nisus* (Newton 1991, 1993) and Merlins *Falco columbarius* (Wiklund 1996), but it seems to be practical to discuss these components separately.

Differences in site quality have been shown in a wide variety of species, different seasons, regions and activities (e.g., Newton 1976a; Toland 1987; Kostrzewa 1996; Pavey & Smyth 1998; Franklin *et al.* 2000; Jenkins 2000), although the spatial variation can be smaller than temporal (McClaren *et al.* 2002, but see Franklin *et al.* 2000) and site characteristics may explain different amounts of variation for different species (Krüger 2002). The evidence of whether raptors and owls use habitats preemptively (i.e. occupy best sites first, making them unavailable for other individuals; Pulliam & Danielson 1991) is more equivocal. Six studies demonstrated that after experimental removal of individuals (Newton 1991; Ardia & Bildstein 1997).

persecution and/or pollution-caused population declines (Mearns & Newton 1988; Ferrer & Donazar 1996; Haller 1996; Löhms 2001), the re-occupancy of sites was not random, being related to certain habitat characteristics and higher success in the preferred sites. The three latter studies (as well as Ueta 2000) reported declines in mean young production during population increase, which in Spanish Imperial Eagles *Aquila adalberti* (Ferrer & Donazar 1996) and Ospreys (Löhms 2001) were due to the addition of suboptimal sites. In contrast, Fernández *et al.* (1998) found that high densities of Griffon Vultures *Gyps fulvus* were also related to lower productivities in traditional sites, probably due to interference in the communal foraging sites of the species. However, the productivity of strictly territorial Golden Eagles has also suffered from intruders' interference (Jenny 1992; Haller 1996). Thus, deviations from preemptive habitat use by birds of prey seem to depend on species and population density, which determine how much settled birds are influenced by others.

Interestingly, site-dependence has not been found in nesting harriers: (1) the newcomers in increasing Marsh Harrier *Circus aeruginosus* populations settled to distinct sites, but productivity did not differ clearly between traditional and new sites, and did not decline in general (Altenburg *et al.* 1987; Underhill-Day 1998); (2) Hen Harriers *Circus cyaneus* were more productive in wet sites but these were not occupied first in spring (Simmons & Smith 1985). However, all these studies described only immediate surroundings of nests, which may not reflect the main factors of success (e.g., food; see Amar & Redpath 2002).

In accordance with the site-dependence concept, nesting Sparrowhawks and Black Kites *Milvus migrans* moved from poor- to high-quality sites during life (Newton 1991; Forero *et al.* 1999). The direct causes of this unidirectional shift were the experience of nesting failure and mate loss (Forero *et al.* 1999), which may be ultimately related to site characteristics. Consequently, better territories show lower turnover rates and are occupied by older birds (Newton 1993). However, the frequency of such shifts is likely to vary widely according to general nest site tenacity (Newton 1979), saturation level (Simmons 1993a) and established territory borders (Selås 1997; Rohner & Krebs 1998) in the population. For example, non-breeding raptors track the appearance of prey-rich patches more effectively than breeders do (Norrdahl & Korpimäki 1996).

## **2. Habitat quality vs individual quality.**

As indicated in the previous paragraph, individual quality and habitat quality may interact. The few relevant raptor habitat studies have measured individual age, body mass or morphometry. Older females have been recorded as occupying better sites in Cooper's Hawk *Accipiter cooperii* (Moore & Henny 1984) and Sparrowhawk (Newton 1991), but not in the Peregrine (Mearns & Newton 1988) and probably not in the Spotted Owl (Franklin *et al.* 2000). In Tengmalm's Owl and Merlin, only older males were likely to occupy better territories (Korpimäki 1988; Hakkarainen & Korpimäki 1996; Wiklund 1996). Body mass or measurements were related to site quality in female, but not male, Tengmalm's Owls (Korpimäki 1990; Hakkarainen & Korpimäki 1996), while the relationship has not been found in Cooper's Hawk (Rosenfield & Bielefeldt 1999) and Eurasian Kestrel (Valkama & Korpimäki 1999). These data demonstrate that (1) the habitat\*individual quality interaction may depend

on sex, due to different experience and role while breeding (e.g. Korpimäki 1990; Forero *et al.* 1999); (2) no study has shown that quality differences between sites could be entirely attributed to individual characteristics, but some have failed to show the role of the latter. Note that two listed studies (Korpimäki 1990; Rosenfield & Bielefeldt 1999) have measured habitat 'quality' only by occupancy and should be interpreted cautiously.

### 3. Sources, sinks, and ecological traps.

Individual sites can be grouped according to habitat characteristics (habitat type) or location (population). If such a grouping follows the distribution of important conditions or resources, one can detect habitat quality differences at the landscape scale – the arena where the net production of offspring ('sources' and 'sinks'; Pulliam & Danielson 1991) or density relative to quality ('ecological traps'; Gates & Gysel 1978) have traditionally been explored. However, in the light of the site-dependence concept, sources, sinks and ecological traps ultimately occur at the scale of individual sites, and landscape-scale effects are only a special case (Rodenhouse *et al.* 1997). In raptors, both local clumping (Ferrer & Donazar 1996; Steiner 1999) and interspersal of high-quality territories (Newton 1991) have been shown. In the latter case, landscapes may still differ at a larger scale (Newton 1976b).

Among 25 landscape-scale studies of 21 species of birds of prey, 14 found higher densities accompanied with higher average success. This included the only study that did not explore reproduction (Mañosa *et al.* 1998 reported a higher proportion of full-cropped birds in densely populated dispersal areas of Bonelli's Eagles *Hieraetus fasciatus*). Eight studies found differences in density but not in productivity, but none of these checked test power to assess statistical errors. There were no clear differences in the species composition or environments between these two types of responses. However, two studies supported the absence of density-productivity relationship in the Golden Eagle: densities differed but productivities did not in the Alpine landscapes (Pedrini & Sergio 2001, 2002), and density and productivity were related to different food sources in Scotland (Watson *et al.* 1992). This probably reflected a trade-off between winter survival of adults and reproductive success in an area (Watson *et al.* 1992), which means that productivity is not a sufficient measure of habitat quality for strongly sedentary species (see also below). Such a trade-off may also reject two 'ecological traps' – lower productivity in dense urban populations of resident raptors (Boal & Mannan 1998, 1999; Salvati 2001), although data for the Eastern Screech-owl *Otus asio* (better productivity and lower survival in a dense suburban than in a rural population; Gehlbach 1988) do not support this explanation, and productivity is inversely related to density also in the partly migratory Wahlberg's Eagle *Aquila wahlbergi* (Simmons 1993b).

Unfortunately, it is not known whether the reported 'ecological traps' were also population 'sinks', since the net production of offspring has been seldom evaluated for different habitat types. In the Barn Owl *Tyto alba*, de Bruijn (1994) described a low-density sink-landscape, where both productivity and mortality exceeded that of a high-density 'source'. Etheridge *et al.* (1997) demonstrated a persecution-caused population sink for Hen Harriers on

Scottish grouse moors, while Ridpath and Brooker (1986) suggested a sink for Wedge-tailed Eagles *Aquila audax* in two West-Australian habitat types. Finally, Newton (1991) reported that, taken individually, nearly half of nesting places were ‘sinks’ for the Sparrowhawk.

4. While sites are of such different quality, species should have evolved abilities to recognize and ultimately use the best sites. The **development of site-quality recognition** seems to include several mechanisms in birds of prey. Innate ‘templates’ or early experiences from birthplace are likely to determine the later nest site use (Table 3), which may explain ‘traditional’ (Newton 1976a; Kirmse 1994) or aberrant nest-sites (Snyder *et al.* 1986) and accidental spread of new nest types (Henny & Kaiser 1996). In contrast, perch use (Grubb *et al.* 1988) and foraging sites seem to be much more influenced by recent experience as raptors often return to successful foraging sites (Wakeley 1978; Sonerud *et al.* 1986), and I already mentioned the importance of learning from negative experience in the life-long search for better territories. These learned behaviours may be related to conditions or resources, which are more difficult to assess by raptors, such as food abundance (cf. Bourne 1985; Beier & Drennan 1997) or predation risk.

**Table 3. Nest-sites of raptors and owls in relation to the sites where they fledged. The numbers denote individuals (except Shutt & Bird 1985, where pairs counted). Note the unchanged preference for nest-boxes in *Falco sparverius* and *F. tinnunculus*, and the importance of fledging habitat for the other species.**

Species	Fledge site	Nest-site		Source
		(a)	(b)	
<i>Accipiter cooperii</i> (wild)	(a) plantation	5	1	Rosenfield <i>et al.</i> 2000
	(b) native forest	1	9	
<i>Falco tinnunculus</i> (captive)	(a) nest-box	5	0	Reifinger 1989
	(b) platform*	5	1	
<i>Falco sparverius</i> (captive)	(a) nest-box	15	0	Shutt & Bird 1985
	(b) ledge	7	0	
<i>Falco peregrinus</i> (wild)	(a) cliff	14	4	Tordoff <i>et al.</i> 1998
	(b) building	4	111	
<i>Falco peregrinus</i> (wild)	(a) urban	9	0	Cade & Bird 1990
	(b) other	7	37	
<i>Tyto alba</i> (captive)	(a) type I	12	0	Schaden 1992
	(b) type I + type II demonstrated*	2	9	

\* since the 3rd week of life

THE GAPS

Below, I discuss four major gaps in knowledge, the exploration of which could significantly enhance both theoretical understanding and species management. At least three of these issues could benefit from meta-analysis of published research (plus careful planning of new studies) since the necessary scale is difficult to reach in any single study.

## 1. Sources and patterns of interspecific, geographic and temporal variation in raptor-habitat relationships.

Habitat variation in general has received little attention (see above), despite the growing evidence of intraspecific differences, such as geographically or annually different habitat use, preferences and quality. Moreover, the increasing number of threatened species can hardly ever be equally well-studied, and managers often have to use information from other species, areas or periods. There is an urgent need for meta-analyses recording similarities and explaining differences in the huge amount of existing information. For example, in order to explore microclimatic effects, hundreds of papers list directions of exposure in raptor habitats. Yet the predictive power for this characteristic is mostly restricted to a few reports that in cold climate or high elevations raptors tend to prefer sun-exposed sites while the opposite is true in hot climate or low elevations (Mosher & White 1976; Snyder *et al.* 1986), that wind or the availability of sheltered nest sites may locally modify these general preferences (Wink *et al.* 1982; Grebence & White 1989), and that the relevant energetic considerations are related to the body mass of species (Poole & Bromley 1988). Altogether, I found only 13 case studies that explicitly explained habitat use via morphology; the scarcity of reports about geographic variation has been mentioned above. Only the annual variation in raptor-habitat relationships has been recently reviewed (Löhmus 2003), but not quantitatively.

2. Meta-analyses could also significantly improve the understanding of **adaptivity of habitat preferences**, which may be classified to at least three types: adaptive (preferred habitats are also better), non-adaptive (preferred habitats are worse), and neutral choices (preferred habitats are neither better nor worse). The latter may be retained through tradition (e.g. Newton 1976a), due to time-lags in response to environmental change (Donazar *et al.* 1993a) or it can be a part of an adaptive strategy to 'buffer' individuals against unpredictable or rare depressing conditions, which are not expressed in all situations (cf. Forbes & Ydenberg 1992). For example, preferences for nest exposure in Black Kites were related to higher hatching success in a dry year but not in two other years (Viñuela & Sunyer 1992).

Given this framework, I checked 90 studies, which explored simultaneously preferences and fitness-correlates of individual locations or home-ranges. I omitted 17 reports which did not discover any effects or where different variables were related to preferences and 'fitness'. Among the remaining 73 studies, there was no clear evidence for non-adaptive choice. Although four studies (Andrew & Mosher 1982; Donazar *et al.* 1993b; Miller *et al.* 1997; Thome *et al.* 1999) found at least one contradiction between habitat preferences and quality, these were either of doubtful biological significance or could be random errors among multiple tests (see above). In contrast, at least some preferences and quality differences coincided and no opposite evidence was given in 39 studies. Twenty-four studies found preferences but no fitness-correlates, and in 12 studies preferences were more numerous than quality-effects, as opposed to only three papers reporting quality-effects but no preferences.



Although the cross-tabulation suggests that habitat selection in raptors and owls is predominantly adaptive and/or neutral, this is only a starting point for further work – serious methodological concerns do not allow one to distinguish the alternatives so easily. First, there is a high possibility of any ‘effects’ being random errors as discussed above. In fact, very few adaptive responses have been reported in more than one paper. An outstanding exception is the selection of high cliffs by nesting Peregrine Falcons as reflected in (1) nest-site preferences at various spatial scales on three continents (Jenkins 1994; Mooney & Brothers 1987; Mearns & Newton 1988; Norriss 1995; Moore *et al.* 1997), (2) sequential occupation during population change (Ellis 1982; Mearns & Newton 1988), and (3) benefits for foraging success (Jenkins 2000) and productivity (Mearns & Newton 1988). Even urban Peregrines prefer the highest buildings for nesting (Cade & Bird 1990)! Second, the sample sizes, and consequently tests’ power, are often lower for productivity than preference analyses (noticed by e.g. Ward *et al.* 1998; Folliard *et al.* 2000), which may give a false impression of a neutral strategy. Oddly, the conclusion may also depend on statistical methods, since Suárez *et al.* (2000) reported 10 univariate preferences and 2 fitness-correlates (both in the ‘adaptive’ direction) of nesting Booted Eagle *Hieraetus pennatus*, whereas the relevant stepwise logistic regression models included a near-equal number (5 and 4, respectively) of non-coinciding variables. Here, the univariate analysis would classify as neutral and adaptive, whereas the multivariate approach does not allow any conclusions.

3. **Trade-offs in habitat selection** are increasingly accounted for in multivariate models but are seldom further explored and generalized. Yet such generalizations could be of great practical value. There may be, for example, compensatory effects, such as (1) the growing need by Bald Eagles for forest cover in more developed areas, probably to provide visual screening and to keep eagles from being frightened away (Chandler *et al.* 1995); or (2) the critical importance of sheltered nest sites to Eleonora’s Falcons *Falco eleonorae* on an islet, where they had to nest on sun-exposed slopes to avoid strong winds from the other side (Wink *et al.* 1982).

Clarification of trade-offs could add significantly also to the studies on adaptivity, since the situations analysed for adaptivity are mostly pieces in the mosaic of trade-offs. In a recent paper, Franklin *et al.* (2000) reported that Spotted Owls had the highest survival in interior forest areas with some edge, but highest fecundity in edge-rich areas with small amounts of forest interior. Clearly, selection of home-range by this resident species includes a compromise between survival and reproduction requirements (see also Carey & Peeler 1995), and a study of adaptivity may reach different conclusions depending on which life-history parameters are addressed.

4. Most studies about **the impact of habitat loss and fragmentation** (habitat loss thresholds, effects of patch size and isolation, edge avoidance, landscape diversity) on birds of prey have yielded vague and contrasting conclusions. In my opinion, this field suffers from the absence of a general view of what constitutes habitat patch for a raptor. Many researchers equalize ‘habitat’ and ‘vegetation type’, but the habitat (*sensu* Hall *et al.* 1997) of most raptors contains several vegetation types. A bird that breeds in the edge of a

forest adjacent to a grassland used for foraging is a *forest edge species* but breeds in the *interior of its habitat patch*, and its area requirements are defined by both forest and grassland. The conceptual vagueness is likely to shadow several generalizations about raptors. For example, the rule that generalist raptors are more readily found in mosaic habitats and avoid the areas of decreased habitat diversity (Donázar *et al.* 1997), may theoretically include specialist species that need more than one vegetation type – a habitat that is lost in homogeneous landscapes. Similarly, the idea that for area-sensitive species habitat models explain larger amounts of variance in their occurrence or fitness (Krüger 2002) may simply reflect the fact that researchers are able to measure relevant habitat variables better for some species than for others. No surprise that the most promising attempts to explore habitat-loss thresholds have either used a species that is restricted to few distinct vegetation types (Lamberson *et al.* 1992; Swindle *et al.* 1999) or explored a ‘non-habitat’ area (e.g. the immediate effects of afforestation or urbanization: Newton *et al.* 1982; Watson 1992; Bosakowski & Smith 1997; Berry *et al.* 1998)! To summarize, a conceptual clarification could significantly enhance the treatment of habitat loss in raptors.

## CONCLUSIONS

During the last decades an impressive number of raptor habitat studies have been produced, and many methodological problems have been increasingly well addressed. Nevertheless, species and regions are very unevenly represented, and many of conservation concern have not been explored at all. Moreover, raptor-habitat relationships vary widely between species, sites and periods. This variation is interesting, but it can be a nuisance for conservationists suffering from the lack of representative and detailed data. Hence, the issue of critical importance is whether, and how, is it possible to use the knowledge from previous case studies to solve new problems. Up to now, generalizations have been obvious in only a minority of studies, and have been paradoxically rare in the extensively explored cases (e.g. the Spotted Owl studies in the U.S.) which could have given useful rules for other systems. Yet generalizing is not an easy task and clearly has its limits as a surrogate of original studies.

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