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REVIEW

The breeding performance of raptors in urban landscapes: a review and meta-analysis

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Abstract Global urbanisation is rapidly increasing and can have profound impacts on wild flora and fauna. For many species, the impacts are detrimental and irreversible, whereas others are able to colonise and apparently thrive in these novel, human-made environments. Raptors are particularly susceptible to changes in the environment due to their position at the end of the food chain, yet some species are increasingly associated with towns and cities. To explore the impact of urbanisation on raptors, we reviewed the literature and compared breeding performance in urban and rural populations globally. In general, raptors began breeding earlier and had larger brood sizes in urban compared to rural environments. However, some of these raptors also fledged fewer young in urban habitats, apparently caused largely by a lack of prey and, in some cases, increased human disturbance. As such, urban environments may act as ecological traps for some raptor species. Species differed in their response to urbanisation. In particular, specialist bird predators such as Peregrine Falcons (*Falco peregrinus*) had a higher breeding performance (clutch size, brood size, number to fledge and nest success) and showed a positive response to urbanisation compared to those that predate on small mammals, such as Eurasian Kestrels (*F. tinnunculus*), which showed a negative response. This suggests that prey availability is one of the

most important determinants of the success of urban-nesting raptors. We demonstrate a need for continued research into the breeding performance of raptors that live in urban environments, and stress the importance of focusing on the reasons for any differences in breeding performance between urban and non-urban environments in order to aid conservation and management efforts for this iconic bird group.

Keywords Urban ecology · Avian conservation · Urbanisation · Productivity · Bird of prey

Zusammenfassung

Brutleistung von Greifvögeln in städtischen Landschaften: Überblick und Meta-Analyse

Global nimmt die Urbanisierung rapide zu und kann wesentlichen Einfluss haben auf Flora und Fauna. Für viele Arten sind die Auswirkungen schädlich und unumkehrbar, während andere in der Lage sind, sich anzusiedeln und in diesen neuen anthropogenen Umgebungen aufzublühen. Greifvögel sind aufgrund ihrer Position am Ende der Nahrungskette besonders empfindlich für Veränderungen in der Umwelt, und trotzdem sind manche Arten zunehmend typisch für städtische Umgebungen. Um den Einfluss der Urbanisierung auf Greifvögel zu untersuchen, gingen wir die Literatur durch und verglichen die Brutleistung in urbanen und ländlichen Populationen weltweit. Insgesamt begannen Greifvögel früher zu brüten und hatten größere Bruten in städtischen im Vergleich zu ländlichen Umgebungen. Allerdings wurden bei einigen der Greifvögel weniger Jungtiere flügge in urbanen Umgebungen, anscheinend größtenteils aufgrund von Beutemangel und, in manchen Fällen, stärkerer

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Störung durch Menschen. Insofern könnten städtische Umgebungen als ökologische Falle für manche Greifvogelarten wirken. Die Arten unterschieden sich in ihrer Reaktion auf die Urbanisierung. Insbesondere hatten Arten wie der Wanderfalke (*Falco peregrinus*), deren Hauptbeute Vögel sind, eine höhere Brutleistung (Gelegegröße, Brutgröße, Anzahl von flüggen Jungvögeln und Bruterfolg) und zeigten eine positive Reaktion auf die Urbanisierung, im Gegensatz zu Arten, die im wesentlichen auf Kleinsäuger jagen wie der Turmfalke (*F. tinnunculus*), die eine negative Reaktion zeigten. Das legt nahe, dass die Verfügbarkeit von Beute eine der wichtigsten Determinanten ist für den Erfolg von stadtbrütenden Greifvögeln. Wir zeigen die Notwendigkeit einer fortgesetzten Erforschung der Brutleistung von Greifvögeln in Städten auf und betonen die Notwendigkeit, sich auf die Gründe für jegliche Unterschiede in der Brutleistung zwischen urbanen und ländlichen Umgebungen zu konzentrieren, um die Bemühungen um Schutz und Management dieser Vogelarten zu unterstützen.

Introduction

Approximately 54% of the world's human population currently live in towns or cities (United Nations 2015). As the global human population continues to grow, the area of urban land cover increases and natural habitats are transformed into human-made systems (Gaston 2010). The process of urbanisation can alter species assemblages, resulting in changes in trophic networks such as the abundance of parasites and disease (Bradley and Altizer 2007). Urbanisation can have profound environmental consequences, including a decline in population densities, species richness and composition, and the extinction of species (Marzluff and Ewing 2001; Gaston 2010; Gil and Brumm 2014). Conversely, some species are able to colonise, persist and even thrive in these 'novel' urban environments (Shanahan et al. 2014). Indeed, it is now commonly acknowledged that species respond to urbanisation in three distinct ways: those that 'avoid', 'adapt' to, or 'exploit' urban areas (Blair 1996; McKinney 2006). Although there is an increasing focus on the ecological responses of various taxa to urbanisation (e.g. Wang et al. 2001; Marchand and Litvaitis 2004; Wania et al. 2006; Hamer and McDonnell 2008; Ahrné et al. 2009; Vermonden et al. 2009; Bateman and Fleming 2011), the majority of studies appear to focus on birds (Chace and Walsh 2006).

Urban adapters and exploiters may benefit from a number of factors associated with urbanisation. For

example, supplementary feeding of wildlife, in particular birds, is now commonplace in urban areas. Supplementary feeding is thought to be one of the main factors increasing avian populations (Amrhein 2014). In fact, the density of birds, in particular some passerine species and Feral Pigeons (*Columba livia*), is thought to increase with urban cover due to the association with higher food abundance (Blair 1996; Marzluff 2001; Tratalos et al. 2007). Furthermore, the migratory behaviours of some species may be altered due to the increased consistency and abundance of food (Plummer et al. 2015). Urban environments may also present some species with increased nesting habitat, including natural vegetation and artificial nest boxes (Harper et al. 2005; Jokimäki et al. 2016, 2017). However, the benefits of urban-living can often be short-lived due to a number of limitations associated with urbanisation. Indeed, some species are thought to have fallen into an 'ecological trap', whereby the urban habitat appears attractive but is actually of relatively poor quality (e.g. Sumasgutner et al. 2014a; Russo and Ancillotto 2015; Demeyrier et al. 2016). For instance, increased human disturbance associated with urban areas, including pedestrian traffic, has been found to reduce nest spacing (Fernández-Juricic 2002), species density (Fernández-Juricic and Tellería 2000) and species richness (Schlesinger et al. 2008). The introduction of non-native predators (Bonnington et al. 2013; Loss et al. 2013), collisions with buildings and vehicles (Erritzoe et al. 2003; Bishop and Brogan 2013), and pollution (Fuller et al. 2007; Kempenaers et al. 2010; Isaksson 2015) have also been shown to have negative effects on the health, survival and reproduction of urban wildlife.

The responses of predatory species to urbanisation are particularly interesting due to their susceptibility to changes in the environment and the cascading effects on biotic community structures (Newton 1998; Fischer et al. 2012). Although the density of some predatory species may increase along an urbanisation gradient, some apex predators that require large home ranges and have specialist diets are largely absent in the urban core (Fischer et al. 2012). However, raptors are increasingly associated with towns and cities and some species have colonised even the most urbanised areas (e.g. Martin et al. 2014; Sumasgutner et al. 2014a; Mazumdar et al. 2016). Indeed, urban environments are thought to offer 'superior quality' habitat to some raptor species due to a high abundance of prey (Chace and Walsh 2006). However, raptor species differ in their dietary and habitat requirements, breeding ecology and home range sizes, and thus may face varying challenges associated with urbanisation. For instance, infectious diseases are thought to be prevalent in some urban-nesting raptors (e.g. Krone et al. 2005) but not in others (e.g. Suri et al. 2017). Moreover, raptors face

additional threats such as persecution (e.g. Etheridge et al. 1997; Smart et al. 2010; Amar et al. 2012) and collisions with human-made structures (Hager 2009). Measuring the responses of raptors to urbanisation is thus important in order for suitable management efforts to be implemented.

The amount of research conducted on raptors, including how they have adapted to human-dominated environments, has grown rapidly in recent years (Donazar et al. 2016). This study summarises the responses of this bird group to urbanisation, using breeding performance as a proxy for habitat quality. We concentrate on a number of parameters in order to assess breeding performance in various raptor species: clutch size, brood size, number of young to fledge and success of nests. These breeding parameters are negatively affected by urbanisation in other bird groups, such as passerines. In many cases, this is thought to be due to a lack of natural food (Chamberlain et al. 2009). Prey availability is thought to strongly shape the breeding performance of raptors (Newton 1979), which is expected to differ between urban and rural environments in response to the likely difference in prey availability and/or quality (Marzluff and Ewing 2001; Shochat et al. 2006). However, raptor species vary in their feeding habits from generalist to specialist hunters (Newton 1979), thus their ability to adapt to novel conditions may also differ (e.g. Berry et al. 1998). For instance, some may specialise in hunting birds, small mammals or insects, whilst others feed on a variety of prey. Because of the varying responses of different taxa and species to urbanisation, predator-prey dynamics are often shifted in urban environments (Fischer et al. 2012). As such, we look at the responses of raptors based on their dietary requirements in order to understand patterns in more depth. We also examine the timing of breeding in urban and non-urban habitats, as Chamberlain et al. (2009) found urban-nesting passerines to breed earlier, triggered by higher temperatures (a consequence of the urban heat island effect), year-round availability of human-provided food and artificial night-lights (e.g. Solonen 2001; Peach et al. 2008; Chamberlain et al. 2009; Kempnaers et al. 2010). With this review, we aim to offer a deeper understanding of how raptors respond to the novel environmental conditions that humans impose on natural landscapes, providing insight into the benefits of urban environments for raptor breeding performance.

Methods

Literature search

A literature search was performed using the Web of Science (<https://apps.webofknowledge.com>) and Google Scholar (<https://scholar.google.co.uk/>) using the search

terms: (bird of prey OR raptor OR hawk OR falcon OR owl OR harrier OR vulture OR eagle OR buzzard OR osprey OR kite) AND (urban*) AND (reproduct* OR productivity OR breeding). A number of key references were also identified from articles found during the search. Books, including edited books on avian urban ecology, were also searched for appropriate studies.

Breeding parameters

Studies that provided separate breeding parameters for paired urban and rural habitats were included in the descriptive analyses (Table 1). Additionally, we included our own data (clutch size, brood size, number of young to fledge and nest success) on urban and rural Peregrine Falcons (*Falco peregrinus*) across the UK, collected by raptor groups between 1996 and 2016. Studies that focused only on urban-nesting pairs were also included in both the descriptive analyses and the meta-analyses, and compared with published findings on rural pairs of the same species. Every attempt was made to match studies in terms of their geographical location, for example those in the same country/state/region (Table 2). Although this approach is limited, as factors other than simply whether raptors nest in urban or non-urban habitats may affect breeding performance (e.g. weather), these comparisons provide an insight into the effects of the different landscape types on breeding performance. To avoid pseudoreplication, when multiple studies were gathered from the same geographical region, the average values of the breeding parameters were used (Table 2). Where studies were believed to be based on the same population, only one study was included to avoid duplicating findings (e.g. Sumasgutner et al. 2014a, b), and only the ones most appropriate for this review were included (i.e. provided estimates for the breeding parameters of interest), including the most recently published or those with the largest sample size. Urban-gradient studies (Table 3) included those that used different urban zones depending on the amount of urban land cover (e.g. Millsap and Bear 2000; Riegert et al. 2010; Sumasgutner et al. 2014a) and the percentage of urban land cover within a certain radius of nests (e.g. Frey et al. 2011; Bionda and Brambilla 2012; Hindmarch et al. 2014). However, studies that used an urban-gradient were not included in formal meta-analyses as, in many cases, no data were given at either end of the gradient (e.g. Millsap and Bear 2000; Hindmarch et al. 2014; Sumasgutner et al. 2014b). Nevertheless, the responses of raptors studied on urban gradients are discussed throughout this paper.

To limit bias, only studies using a similar definition of ‘urban’ or ‘suburban’ were included in analyses. This typically included towns or cities, human population size, or percentage cover of buildings and built-up areas.

Table 1 A summary of the 23 studies that compared urban and rural nesting raptors and the breeding parameters measured, as well as whether independent variables were tested to explain variation in breeding performance

Species	Region of study	Clutch size	Brood size	No. to fledge	Success of nests	Timing of breeding	Causal effects of difference	Sources
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	Florida, USA		✓			✓		Millsap et al. (2004) [1]
Barn Owl (<i>Tyto alba</i>)	Rome, Italy		✓	✓			✓	Salvati et al. (2002) [2]
Burrowing Owl (<i>Athene cunicularia</i>)	Washington, USA	✓		✓	✓	✓		Conway et al. (2006) [3]
Burrowing Owl (<i>Athene cunicularia</i>)	New Mexico, USA			✓	✓		✓	Berardelli et al. (2010) [4]
Burrowing Owl (<i>Athene cunicularia</i>)	California, USA		✓		✓			Trulio and Chromczak (2007) [5]
Cooper's Hawk (<i>Accipiter cooperii</i>)	Arizona, USA	✓	✓		✓	✓	✓	Boal and Mannan (1999) [6]
Cooper's Hawk (<i>Accipiter cooperii</i>)	California, USA			✓				Chiang et al. (2012) [7]
Crested Goshawk (<i>Accipiter trivirgatus</i>)	Central Taiwan				✓	✓	✓	Lin et al. (2015) [8]
Eurasian Kestrel (<i>Falco tinnunculus</i>)	Israel	✓	✓	✓	✓	✓	✓	Charter et al. (2007) [9]
Lesser Kestrel (<i>Falco naumanni</i>)	Spain	✓		✓	✓		✓	Tella et al. (1996) [10]
Lesser Kestrel (<i>Falco naumanni</i>)	Israel			✓			✓	Liven-Schulman et al. (2004) [11]
Mississippi Kite (<i>Ictinia mississippiensis</i>)	Kansas, USA			✓	✓			Parker (1996) [12]
Northern Goshawk (<i>Accipiter gentilis</i>)	Southern Finland		✓					Solonen (2008) [13]
Peregrine Falcon (<i>Falco peregrinus</i>)	North-eastern USA			✓				Gahbauer et al. (2015) [14]
Peregrine Falcon (<i>Falco peregrinus</i>)	Great Britain	✓	✓	✓	✓		✓	Kettel et al. unpublished data [15]
Red-shouldered Hawk (<i>Buteo lineatus</i>)	Ohio, USA			✓				Dykstra et al. (2009) [16]
Red-shouldered Hawk (<i>Buteo lineatus</i>)	Ohio, USA				✓			Dykstra et al. (2000) [17]
Red-shouldered Hawk (<i>Buteo lineatus</i>)	California, USA			✓				Bloom and McCrary (1996) [18]
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Wisconsin, USA		✓					Stout et al. (1998) [19]
Swainson's Hawk (<i>Buteo swainsoni</i>)	Idaho, USA			✓	✓		✓	Alsup (2012) [20]
Swainson's Hawk (<i>Buteo swainsoni</i>)	California, USA				✓			England et al. (1995) [21]
Tawny Owl (<i>Strix aluco</i>)	Southern Finland	✓	✓		✓		✓	Solonen and Ursin (2008) [22]
Tawny Owl (<i>Strix aluco</i>)	Southern Finland					✓	✓	Solonen (2014) [23]

Numbers in parentheses correspond with the reference numbers in Figs. 1, 2, 3, 4, 5 and 6

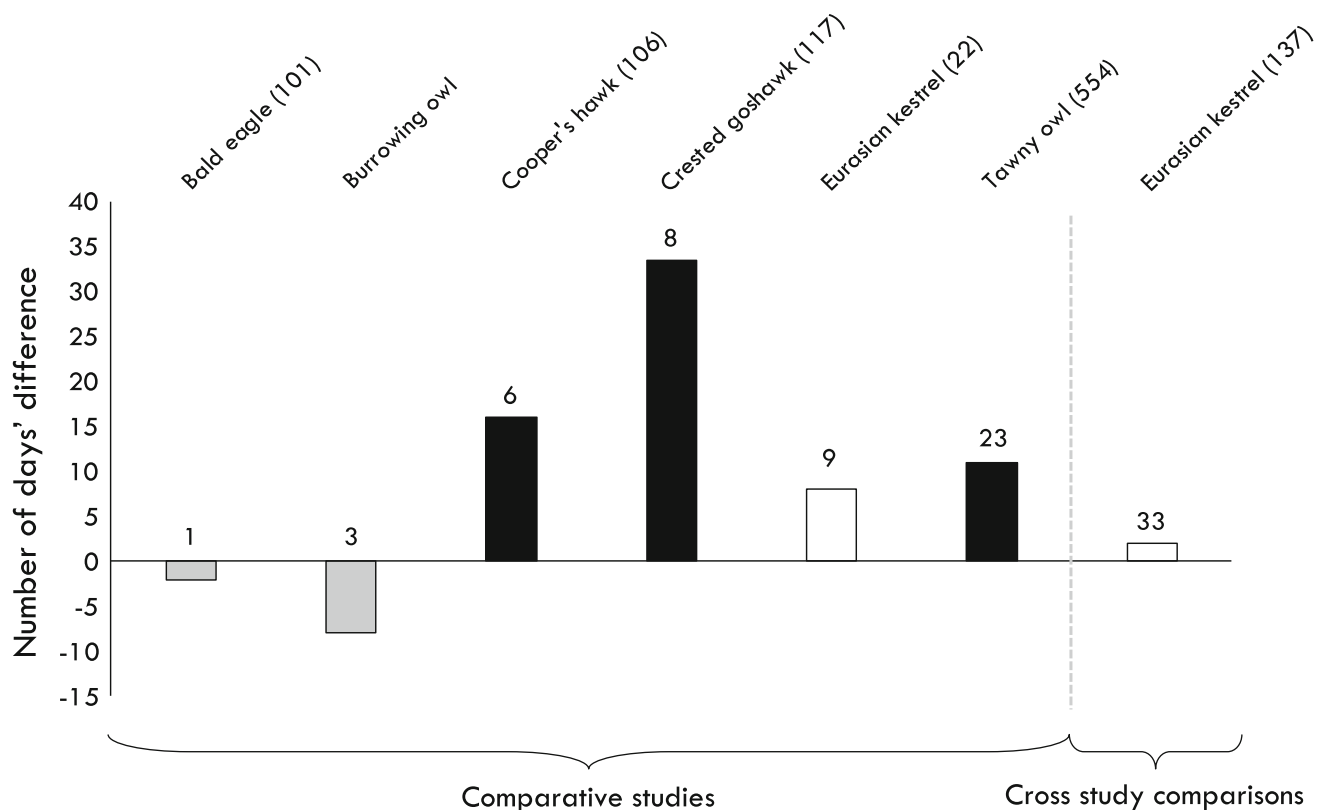


Fig. 1 The number of days' difference in the timing of breeding (start of egg laying/start of egg hatching) between urban and rural nesting raptors of different species where comparisons were made directly in the study (*Comparative studies*) and where comparisons were made between different studies (*Cross study comparisons*). Positive values indicate a positive response to urbanisation and negative values indicate a negative response. Black bars indicate a

significant difference, grey bars represent a non-significant difference, and white bars indicate that no statistical tests were undertaken in the studies. Numbers above bars represent the source of the study as shown in Tables 1 and 2, and numbers in parentheses show the sample sizes of urban and rural nesting attempts combined in the studies

However, definitions of a rural habitat differed between studies due to the diversity of habitats. For example, in Charter et al.'s (2007) study on Eurasian Kestrels (*F. tinnunculus*), rural habitat was defined as small villages with few buildings and a human population size smaller than 700. Yet in other studies, rural habitat was defined simply as agricultural land (Tella et al. 1996; Alsup 2012; Chiang et al. 2012; Lin et al. 2015) or woodland (Solonen and Ursin 2008), or measured by the intensity of human use (Stout et al. 1998; Millsap et al. 2004). For our own data, urban Peregrine Falcons were defined as those nesting in a city or town, whereas rural ones were defined as those nesting outside of the town or cityscape.

The breeding parameters of interest included: (1) timing of breeding (onset of egg laying or hatching), (2) clutch size (number of eggs per nest), (3) brood size (number of eggs to hatch per brood), (4) number of chicks to fledge the nest, and (5) nest success (whether or not at least one chick fledged, or where at least one chick reached an age at which it was likely to fledge). However, not all studies investigated all parameters (Table 1). For timing of

breeding, either Julian dates (day count beginning at 1 Jan) or calendar dates were used, and the difference in the number of days was calculated. For clutch size, brood size and number of chicks to fledge, the difference between the mean values was calculated by subtracting the mean for rural sites from the mean for urban sites, giving a negative difference where rural environments were more successful. Although comparing raw means from studies can be useful to summarise results, this does not consider sample size [leading to low power (see Stewart 2010)]. Therefore, where means, SDs and sample sizes were given, standardised mean differences were calculated (see Gurevitch and Hedges 2001) so that all studies could be measured and compared in the same way (Sedgewick and Marston 2013), irrespective of mean life history trait values (Gurevitch and Hedges 2001). Studies defined the number of young to fledge using either all nesting attempts or successful nesting attempts only (i.e. produced at least one young to fledge). In some instances, the same study reported on both definitions, thus only the number to fledge from all nesting attempts was used to avoid replication. Studies defined

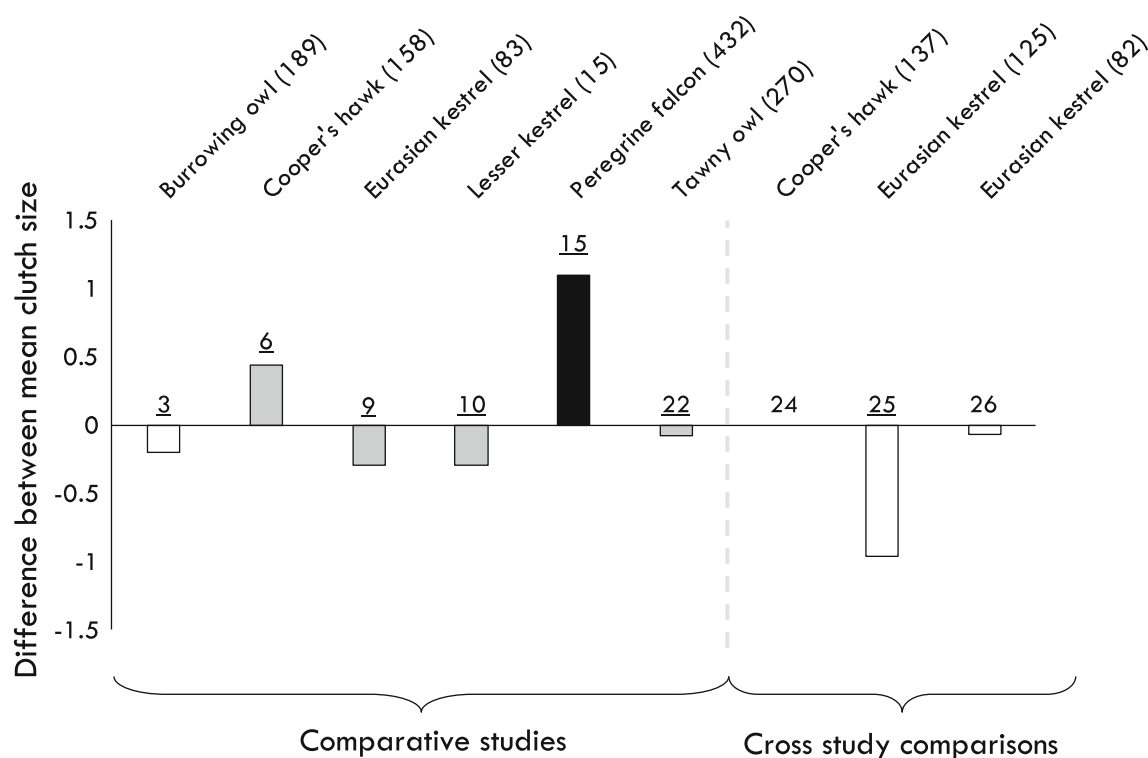


Fig. 2 The differences in mean clutch size between urban and rural nesting raptors of different species where comparisons were made directly in the study (*Comparative studies*) and where comparisons were made between different studies (*Cross study comparisons*). *Positive values* indicate a positive response to urbanisation and *negative values* indicate a negative response. *Black bars* indicate a significant difference, *grey bars* represent a non-significant

difference, and *white bars* indicate that no statistical tests were undertaken in the studies. *Numbers above bars* represent the source of the study as shown in Tables 1 and 2, and *underlined numbers* show which studies were included in meta-analyses. *Numbers in parentheses* show the sample size of urban and rural nesting attempts combined in the studies

successful nesting attempts as either at least one chick to fledge, or at least one chick to reach a certain age at which it was likely to fledge. In most instances, the percentage of successful nests was given, thus the percentage difference between urban and rural habitats could be calculated.

Meta-analyses were undertaken by conducting Z-tests to compare the clutch size, brood size and number to fledge between urban and rural raptors if sample sizes were sufficient (>5 in both urban and rural), by pooling the sample sizes from various studies together. Due to low sample sizes, meta-analyses were not undertaken on studies that looked at the timing of breeding or nest success. Meta-analyses were performed using the systematic review software Review Manager (version 5.3.5). We did not control for phylogeny because there were insufficient numbers of independent lineages to do so efficiently.

In order to understand the reproductive responses of raptors in more depth, species were grouped into their respective families: Accipitridae (hawks, eagles, harriers), Falconidae (falcons) and Stigididae/Tytonidae (owls); and by preferred prey types (bird specialists, small mammal specialists, insect specialists or generalists). Information on

diet and classification was obtained from Snow and Perrins (1997) and the Cornell Lab of Ornithology (2016). Studies that produced higher clutch sizes, brood sizes, number to fledge and nest success in urban areas were assigned a positive response to urbanisation and vice versa. Timing of breeding was not included here as it was not appropriate (i.e. did not provide positive/negative responses). Breeding parameters were combined in the analyses to improve sample size. Differences in these responses were then investigated between the different bird groups (family and diet) using binary logistic regressions in Minitab (version 17.2.2).

Results

Literature search

A total of 23 paired-comparison studies met the criteria for this review. These studies looked at the following breeding parameters: timing of breeding (six studies), clutch size (six), brood size (nine), number of young to fledge (13) and

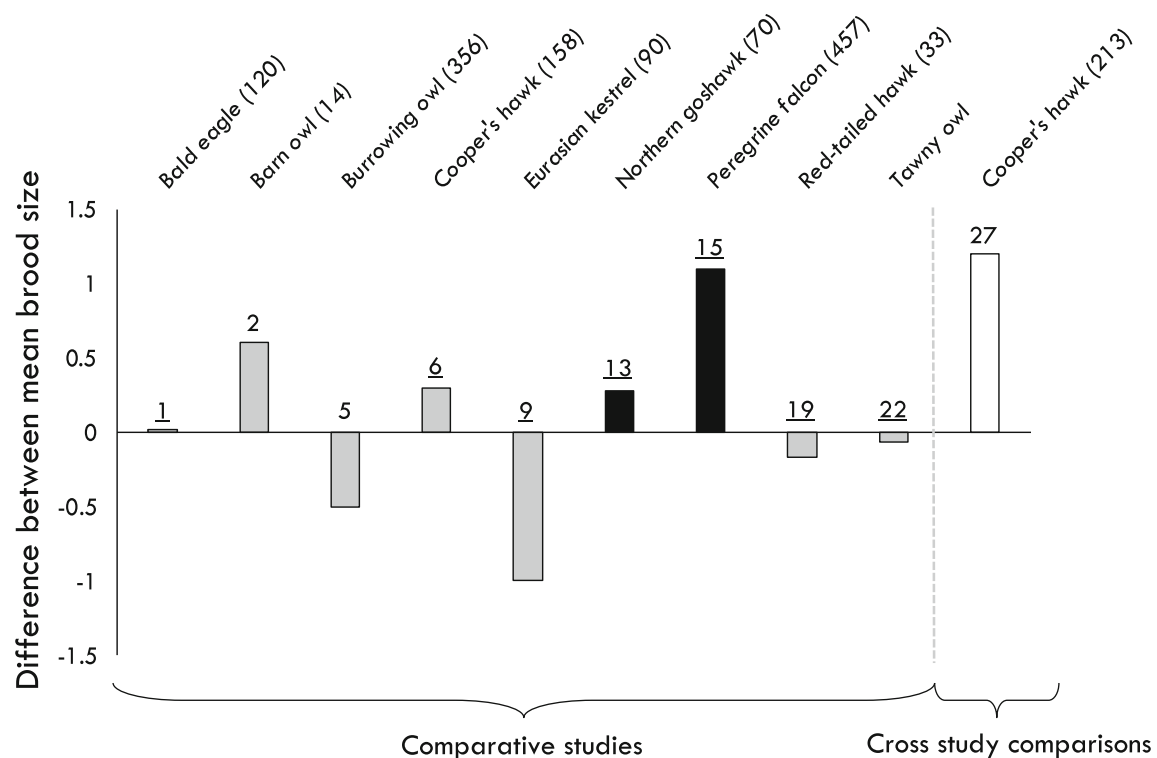


Fig. 3 The differences in mean brood size between urban and rural nesting raptors of different species where comparisons were made directly in the study (*Comparative studies*) and where comparisons were made between different studies (*Cross study comparisons*). *Positive values* indicate a positive response to urbanisation and *negative values* indicate a negative response. *Black bars* indicate a significant difference, *grey bars* represent a non-significant

difference, and *white bars* indicate that no statistical tests were undertaken in the studies. *Numbers above bars* represent the source of the study as shown in Tables 1 and 2, and *underlined numbers* show which studies were included in meta-analyses. *Numbers in parentheses* show the sample size of urban and rural nesting attempts combined in the studies

nest success (13) (Table 1). Six urban-only studies were compared with matched rural-only studies, allowing further comparisons in timing of breeding (two), clutch size (three), brood size (one), number of young to fledge (three) and nest success (two) (Table 2). Eight studies using an urban-gradient were also considered for this review, concerned with timing of breeding (three), clutch size (four), brood size (five), number to fledge (six) and nest success (two) (Table 3).

There was a geographical and species bias as most studies were concentrated in the USA (54% of reviewed studies) and Europe (35%), focussing predominately on Eurasian Kestrels (13.5%), Burrowing Owls (10.8%; *Athene cunicularia*), Cooper's Hawks (10.8%; *Accipiter cooperii*), Red-shouldered Hawks (10.8%; *Buteo lineatus*) and Barn Owls (8.1%; *Tyto alba*; Tables 1, 2, 3).

Timing of breeding

The literature reported that Cooper's Hawks, Crested Goshawks (*Accipiter trivirgatus*) and Tawny Owls (*Strix aluco*) all began breeding significantly earlier in urban

environments (Boal and Mannan 1999; Solonen 2014; Lin et al. 2015). The biggest difference was found in Crested Goshawks, where breeding began over a month earlier in urban nesters (Fig. 1) (Lin et al. 2015). Eurasian Kestrels also began breeding on average 2 and 8 days earlier in urban environments, but the significance was not tested in the comparative study, perhaps due to low sample size (Fig. 1) (Charter et al. 2007). Two studies showed that breeding began later at urban sites, but differences were not significant in these studies (Millsap et al. 2004; Conway et al. 2006). There was no effect of urban land cover on the onset of laying in Barn Owls (Frey et al. 2011), American Kestrels (*F. sparverius*) (Strasser and Heath 2013) or Eurasian Kestrels (Sumasgutner et al. 2014b) when measured on an urban gradient.

Clutch size

Peregrine Falcons were the only species to show a significant difference within the studies in clutch size, producing an average of 1.1 more eggs in urban habitats (Fig. 2) (Kettel et al. unpublished data). Cooper's Hawks also

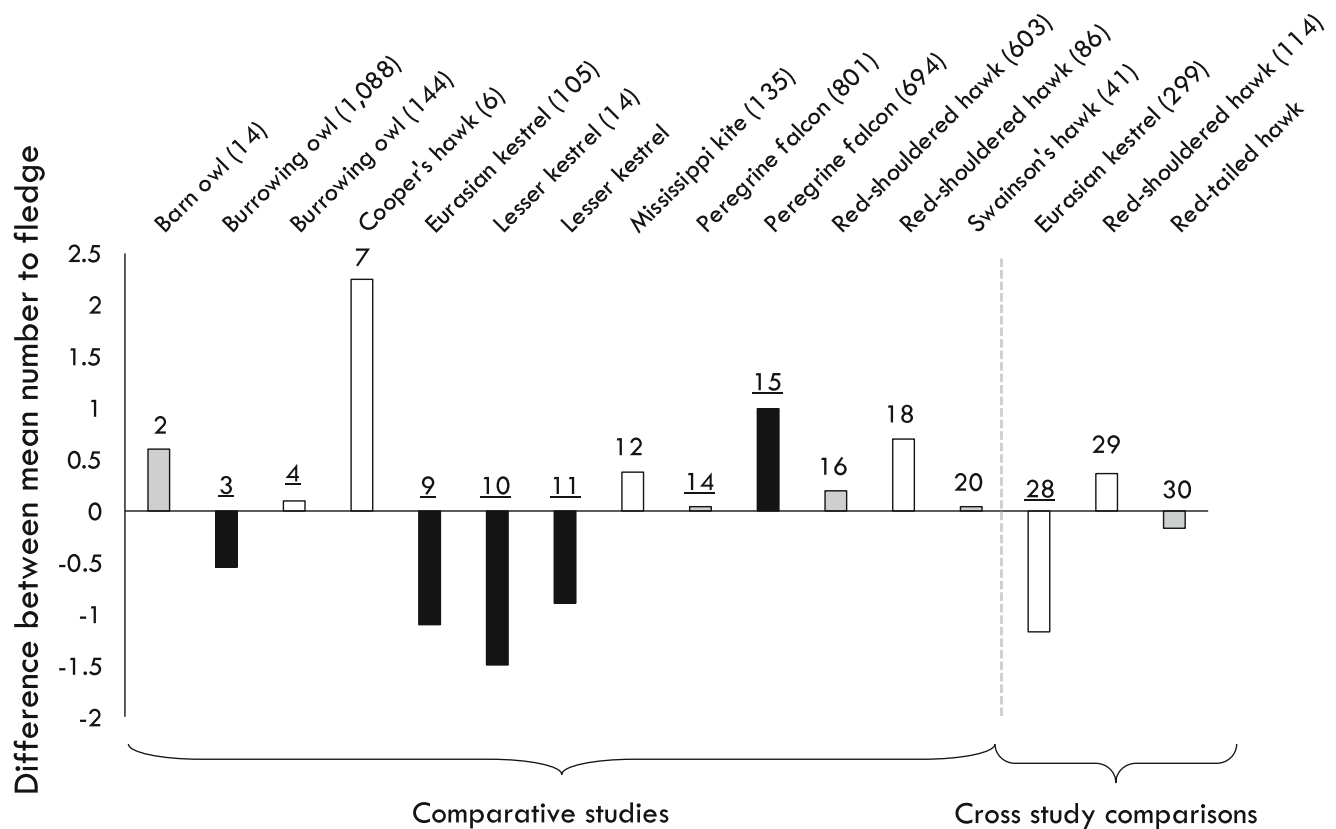


Fig. 4 The differences in the mean number to fledge between urban and rural nesting raptors of different species where comparisons were made directly in the study (*Comparative studies*) and where comparisons were made between different studies (*Cross study comparisons*). Positive values indicate a positive response to urbanisation and negative values indicate a negative response. Black bars indicate a significant difference, grey bars represent a non-significant

difference, and white bars indicate that no statistical tests were undertaken in the studies. Numbers above bars represent the source of the study as shown in Tables 1 and 2, and underlined numbers show which studies were included in meta-analyses. Numbers in parentheses show the sample size of urban and rural nesting attempts combined in the studies

showed a positive response to urbanisation, laying on average 0.44 more eggs in urban areas, but this difference was not significant in the study (Boal and Mannan 1999). However, other findings for Cooper's Hawks showed no difference in clutch size between the habitats when looking at cross-study comparisons (Rosenfield et al. 1996, 2000).

Six studies on clutch size showed a non-significant, negative response to urbanisation (Fig. 2), where Burrowing Owls, Eurasian Kestrels, Lesser Kestrels (*F. naumanni*) and Tawny Owls laid on average 0.2 – 0.3 fewer eggs in urban areas (Tella et al. 1996; Conway et al. 2006; Charter et al. 2007; Solonen and Ursin 2008). Eurasian Kestrels also laid fewer eggs in urban habitats when comparing separate urban and rural studies (Fig. 2; Salvati 2002; Kübler et al. 2005; Carrillo and González-Dávila 2009; Costantini et al. 2014) and were also negatively affected by urban cover in an urban gradient study in Austria (Sumasgutner et al. 2014b). Conversely, another urban gradient study on Eurasian Kestrels in the Czech Republic showed no apparent effect of urbanisation (Riegert et al.

2010), a finding also shown in Barn Owls (Frey et al. 2011; Hindmarch et al. 2014).

Brood size

Six studies showed that more chicks were produced in urban nests. The greatest differences were found in Peregrine Falcons and Cooper's Hawks, where 1.1–1.2 more chicks were produced in urban habitats (Rosenfield et al. 1996, 2000; Kettel et al. unpublished data). Barn Owls, Cooper's Hawks and Northern Goshawks (*Accipiter gentilis*) produced brood sizes of 0.28–0.6 more chicks in urban nests (Fig. 3) (Boal and Mannan 1999; Salvati et al. 2002; Solonen 2008) but Bald Eagles (*Haliaeetus leucocephalus*) produced only 0.02 more chicks in urban habitats (Millsap et al. 2004). Differences were only significant for Peregrine Falcons and Northern Goshawks, despite relatively large sample sizes in the majority of studies (Fig. 3).

Conversely, Burrowing Owls and Eurasian Kestrels produced 0.5 and one fewer chicks, respectively, at urban

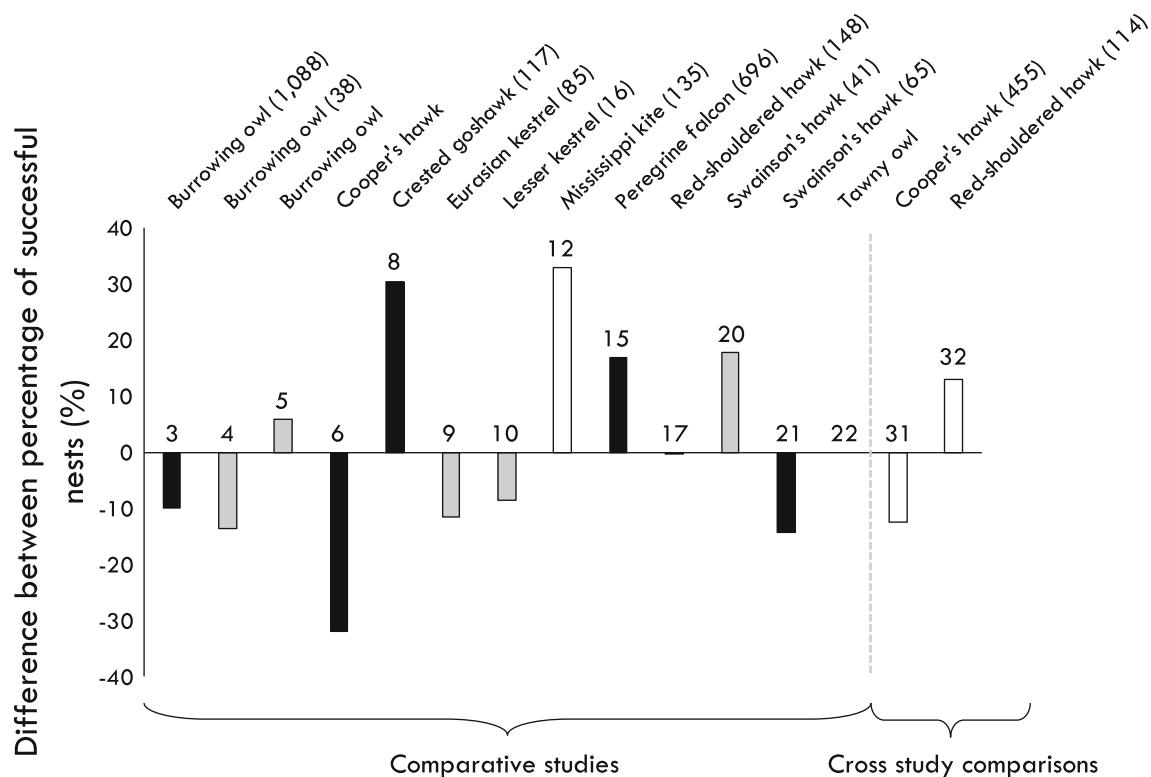


Fig. 5 The differences in the percentage of successful nests between urban and rural nesting raptors of different species where comparisons were made directly in the study (*Comparative studies*) and where comparisons were made between different studies (*Cross study comparisons*). Positive values indicate a positive response to urbanisation and negative values indicate a negative response. Black bars

indicate a significant difference, grey bars represent a non-significant difference, and white bars indicate that no statistical tests were undertaken in the studies. Numbers above bars represent the source of the study as shown in Tables 1 and 2, and numbers in parentheses show the sample size of urban and rural nesting attempts combined in the studies

sites (Charter et al. 2007; Trulio and Chromczak 2007). Red-tailed Hawks (*B. jamaicensis*) and Tawny Owls also had lower brood sizes in urban habitats, but to a lesser extent (Stout et al. 1998; Solonen and Ursin 2008). However, in these latter two studies, samples sizes were small or unknown (Fig. 3). Long-legged Buzzards (*B. rufinus*) and Eurasian Kestrels also showed negative responses to urbanisation, producing fewer eggs with increasing amounts of urban cover (Dermerdzhiev et al. 2014; Sumasgutner et al. 2014b). In another urban-gradient study on Eurasian Kestrels, and in Barn Owls, there was no apparent effect of urban cover (Riegert et al. 2010; Frey et al. 2011).

Number of young to fledge

Ten studies showed a positive response to urbanisation in the number of young to fledge. However, only Peregrine Falcons produced significantly more young to fledge in urban habitats (Kettel et al. unpublished data), and although Cooper's Hawks showed the biggest difference of 2.25 more young fledged at urban nests, this difference was

not significant in this study, probably due to the small sample size [six nesting attempts (Chiang et al. 2012)] (Fig. 4). Barn Owls, Burrowing Owls, Mississippi Kites (*Ictinia mississippiensis*), Red-shouldered Hawks and Swainson's Hawks (*B. swainsoni*) all produced more young to fledge at urban sites, but none of these differences were significant in the studies, despite large sample sizes (Fig. 4; Bloom and McCrary 1996; Parker 1996; Salvati et al. 2002; Dykstra et al. 2009; Berardelli et al. 2010; Alsup 2012). In an urban-gradient study, Burrowing Owls responded positively to urban cover up until their numbers reached high levels and stabilised (Millsap and Bear 2000).

Twelve studies showed a negative response to urbanisation, where Eurasian and Lesser Kestrels, Burrowing Owls and Red-tailed Hawks all produced fewer young to fledge in urban habitats (Fig. 4; Minor et al. 1993; Tella et al. 1996; Salvati 2002; Liven-Schulman et al. 2004; Conway et al. 2006; Charter et al. 2007; Costantini et al. 2014). There were negative responses to urbanisation from Barn Owls, Eagle Owls, Eurasian Kestrels and Long-legged Buzzards with respect to urban-gradients (Bionda and Brambilla 2012; Dermerdzhiev et al. 2014; Hindmarch

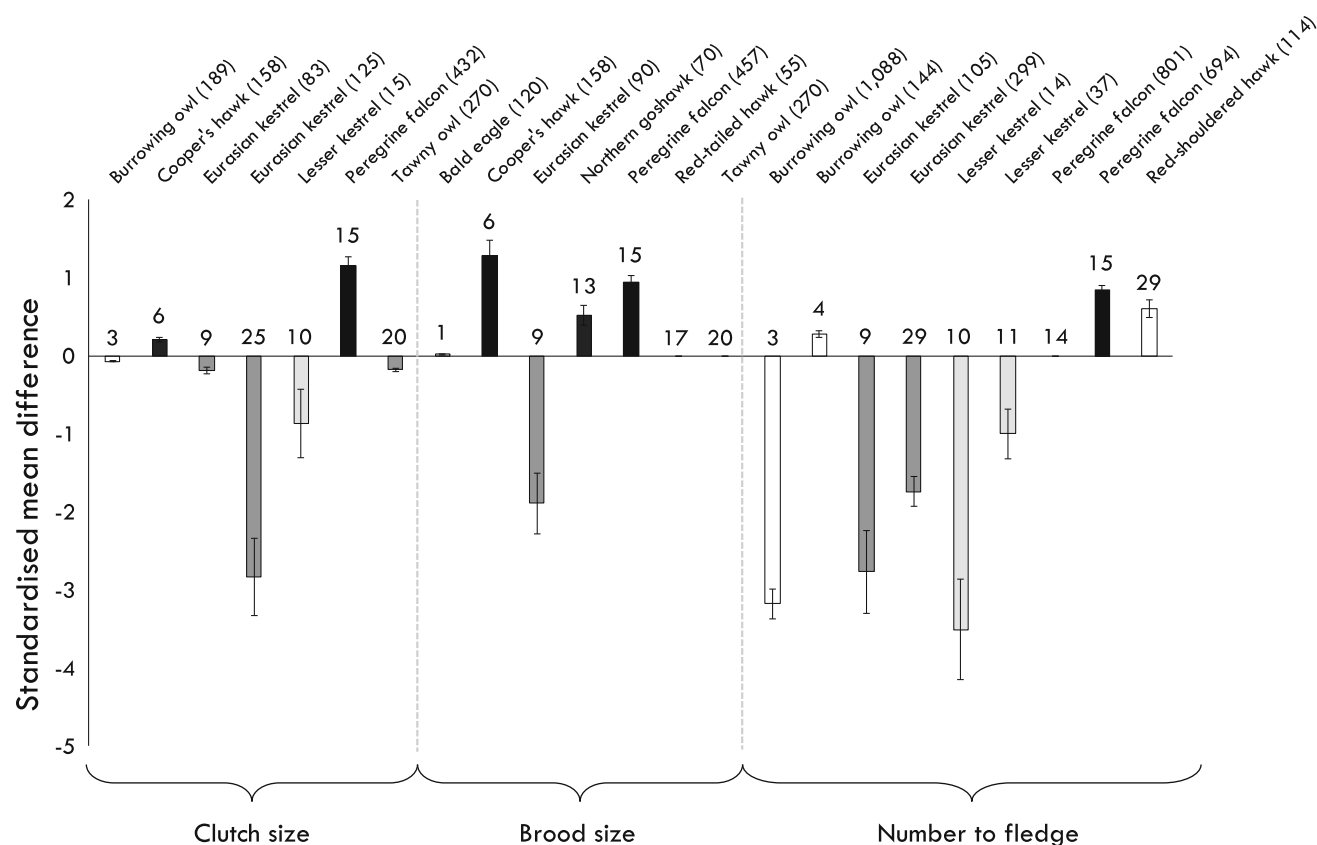


Fig. 6 The standardised mean differences in clutch size, brood size and number to fledge between urban and rural nesting raptors of different species included in meta-analyses. *Positive values* indicate a positive response to urbanisation and *negative values* indicate a negative response. *Numbers above bars* show the source of the study as shown in Tables 1 and 2, and *numbers in parentheses* show the

sample size of urban and rural nesting attempts combined in the studies. *Error bars* represent 95% confidence intervals of the means. *White bars* indicate a generalist feeder, *dark grey bars* indicate small mammal-eating species, *light grey bars* indicate insect-eating species, and *black bars* indicate bird-eating species

et al. 2014; Sumasgutner et al. 2014b). Although, in other urban-gradient studies, there appeared to be no effect of urbanisation on the number of young to fledge in Barn Owls and Eurasian Kestrels (Riegert et al. 2010; Frey et al. 2011).

Nest success

Six studies showed a positive response to urbanisation, with Crested Goshawks and Peregrine Falcons having significantly higher nest success in urban habitats (Kettel et al. unpublished data; Lin et al. 2015) (Fig. 5). Mississippi Kites showed the largest difference, being 33% more successful in urban habitats, but this was not significant, despite a relatively large sample size [135 nesting attempts (Parker 1996)] (Fig. 5). Conversely, Burrowing Owls, Cooper's Hawks, Eurasian Kestrels, Lesser Kestrels and Swainson's Hawks were less successful in urban habitats (England et al. 1995; Tella et al. 1996; Boal and Mannan 1999; Conway et al. 2006; Charter et al. 2007) (Fig. 5) and American Kestrels showed a negative correlation

between nest success and urban cover in an urban-gradient study (Strasser and Heath 2013). However, another study on Burrowing Owls showed no variation in nest success along an urban-gradient (Millsap and Bear 2000).

Meta-analyses

Meta-analyses (Fig. 6) were undertaken using seven studies on clutch size, seven studies on brood size and nine studies on number to fledge. There was no overall effect of urbanisation on the number of eggs laid by raptors ($z = 0.93$, sample size of all studies combined = 1272, $p = 0.35$; Fig. 6), but they produced significantly more chicks in urban areas ($z = 5.59$, sample size of all studies combined = 1220, $p < 0.001$; Fig. 6). Conversely, there was a near-significant trend for raptors as a group to produce fewer young to fledge in urban habitats ($z = 1.88$, sample size of all studies combined = 3296, $p = 0.06$; Fig. 6).

Table 2 Source and location of studies that have measured various breeding parameters in urban locations and the location and source of studies carried out in rural areas used for comparisons

Species [pairing number]	Region of urban study	Region of rural study	Urban study source	Rural study source
Clutch size				
Cooper's Hawk (<i>Accipiter cooperii</i>) [24]	Wisconsin, USA	Wisconsin, USA	Rosenfield et al. (1996) ^a	Rosenfield et al. (2000)
Eurasian Kestrel (<i>Falco tinnunculus</i>) [25]	Rome, Italy	Northern Italy	Salvati (2002) ^b	Costantini et al. (2014)
Eurasian Kestrel (<i>Falco tinnunculus</i>) [26]	Berlin, Germany	Germany	Kübler et al. (2005) ^c	Within Carrillo and González-Dávila (2009)
Brood size				
Cooper's Hawk (<i>Accipiter cooperii</i>) [27]	Wisconsin, USA	Wisconsin, USA	Rosenfield et al. (1996) ^a	Rosenfield et al. (2000)
Number to fledge				
Eurasian Kestrel (<i>Falco tinnunculus</i>) [28]	Rome, Italy	Northern Italy	Salvati (2002) ^b	Costantini et al. (2014)
Red-shouldered Hawk (<i>Buteo lineatus</i>) [29]	California, USA	California, USA	Rottenborn (2000) ^d	Wiley (1975)
Red-tailed Hawk (<i>Buteo jamaicensis</i>) [30]	New York State, USA	North and mid-western USA	Minor et al. (1993) ^e	References within Minor et al. (1993)
Success of nests				
Cooper's Hawk (<i>Accipiter cooperii</i>) [31]	Wisconsin, USA	Wisconsin, USA	Stout et al. (2007) ^f	Rosenfield et al. (2000)
Red-shouldered Hawk (<i>Buteo lineatus</i>) [32]	California, USA	California, USA	Rottenborn (2000) ^d	Wiley (1975)
Timing of breeding				
Eurasian Kestrel (<i>Falco tinnunculus</i>) [33]	Rome, Italy	Northern Italy	Salvati (2002) ^b	Costantini et al. (2014)

Numbers in parentheses correspond with the reference numbers in Figs. 1, 2, 3, 4, 5 and 6

^{a–f}Six separate pairings of urban and rural studies

Table 3 A summary of the eight studies that looked at different breeding parameters along an urban gradient, and whether independent variables were tested to explain variation in breeding performance

Species	Region of study	Clutch size	Brood size	No. to fledge	Success of nests	Timing of breeding	Causal effects of difference	Sources
American Kestrel (<i>Falco sparverius</i>)	Idaho, USA				✓	✓		Strasser and Heath (2013)
Barn Owl (<i>Tyto alba</i>)	British Columbia, Canada	✓	✓				✓	Hindmarch et al. (2014)
Barn Owl (<i>Tyto alba</i>)	Switzerland	✓	✓	✓		✓	✓	Frey et al. (2011)
Burrowing Owl (<i>Athene cunicularia</i>)	Florida, USA			✓	✓		✓	Millsap and Bear (2000)
Eagle Owl (<i>Bubo bubo</i>)	Northern Italy			✓				Bionda and Brambilla (2012)
Eurasian Kestrel (<i>Falco tinnunculus</i>)	Bohemia, Czech Rep.	✓	✓	✓				Riegert et al. (2010)
Eurasian Kestrel (<i>Falco tinnunculus</i>)	Vienna, Austria	✓	✓	✓		✓	✓	Sumasgutner et al. (2014b)
Long-legged Buzzard (<i>Buteo rufinus</i>)	Southern Bulgaria		✓	✓				Dermerdzhev et al. (2014)

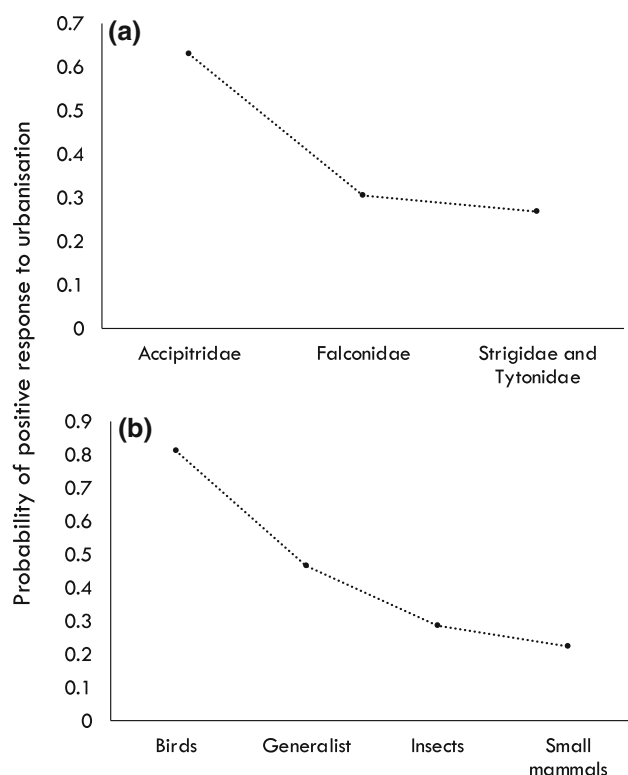


Fig. 7 Probabilities of a positive reproductive response to urbanisation in different raptor families (a) and in raptors that have a main diet of birds, insects, small mammals or are generalist feeders (b)

Differences between bird groups

There was a significant effect of family on the probability of a positive reproductive response to urbanisation ($X^2_{(2)} = 7.60$, $p < 0.05$; Fig. 7a), where the probability of a positive response to urbanisation for Accipitridae was almost twice the probability for Falconidae, Strigidae and Tytonidae (Fig. 7a).

There was also a significant effect of diet on the probability of a positive response to urbanisation ($X^2_{(3)} = 15.71$, $p = 0.001$), where bird-eating raptors had the highest probability, followed by generalists, insect eaters, then small mammal-eating raptors (Fig. 7b). Furthermore, all of the bird-eating raptors included in the meta-analyses responded positively to urbanisation, whilst all small mammal-eating raptors responded negatively (Fig. 6). Indeed, Peregrine Falcons (bird specialists) showed consistency throughout the reproductive parameters, and were found to have a significantly higher clutch size (Fig. 2), brood size (Fig. 3) number to fledge (Fig. 4) and success rate (Fig. 5) in urban areas. Conversely, Eurasian Kestrels (small mammal specialists) also showed consistency but in the opposite direction, indicating a negative response to urbanisation (Figs. 2, 3, 4, 5).

Discussion

The results presented in this review reveal that the reproductive responses of urban raptors are not clear-cut. Findings show considerable disparity between species, specifically between bird and small mammal-eating specialists. Consequently, when observing the response of raptors as a single group, there are no general patterns emerging for clutch size or the success of nests. Nevertheless, there are consistent patterns for raptors to begin breeding earlier and to produce larger broods in urban environments, indicating a positive effect of urbanisation on some species. Persecution has been shown to limit breeding performance of raptors (e.g. Green and Etheridge 1999; Amar et al. 2012), but it is thought that urban-nesters may be more highly protected from this threat (Chace and Walsh 2006). In Crested Goshawks, 56% of failures in rural nests were attributed to predation or harassment by wildlife, whereas predation was not observed in any urban nests (Lin et al. 2015). Similarly, Tella et al. (1996) found that predation was the main cause of death of young Lesser Kestrels in rural, but not urban, habitats (39.5 and 4.6% of deaths, respectively). The installation of artificial nest boxes is also thought to increase the number of young to fledge in some urban-nesting raptors (Altwegg et al. 2014). A combination of these factors may thus result in an increased breeding performance of some raptor species in urban habitats.

Timing of breeding

Raptors showed a strong trend to begin breeding earlier in urban environments (Fig. 1). This finding is similar to that found in passerines, and is hypothesised to be induced by the year-round abundance of food (Solonen and Ursin 2008; Chamberlain et al. 2009). Similarly, the year-round availability of prey in urban environments may allow earlier raptor broods to survive (Lin et al. 2015) and may also promote year-round pair bonds, triggering earlier nesting in raptor species (Boal and Mannan 1999). However, the species studied here were largely resident in the location of study and thus these findings may differ in migratory species who are not influenced by year-round food availability.

Artificial lighting in urban environments has also been suggested to stimulate early breeding in raptors (Solonen 2014), either due to the wrongly perceived length of daylight (Spoelstra and Visser 2014), which has been shown in passerine species (Kempenaers et al. 2010), or by possibly promoting nocturnal hunting and feeding of young (e.g. Kettel et al. 2016). Urban habitats may also act as buffers against fluctuating weather conditions (Solonen 2008;

Solonen and Ursin 2008). For example, Solonen (2008) found that advanced breeding of urban Tawny Owls was in part due to milder winters. Earlier nesting may be beneficial to birds by prolonging the period before the harsher weather conditions of the following autumn/winter, thus increasing the survival of juveniles. Conversely, it may cause asynchronisation with natural food supplies (Crick et al. 1997). The effect that earlier nesting has on urban birds is not entirely understood (Chamberlain et al. 2009) and thus requires further research.

Breeding performance

Despite observed differences between species, the meta-analyses conducted here showed a non-significant trend for raptors to have a lower number of young to fledge from urban nests (Fig. 4), a finding which is again consistent with passerines (Chamberlain et al. 2009). Supplementary feeding of small birds is commonplace worldwide (Jones and Reynolds 2008), and is beneficial to the survival of some passerine species (e.g. Jansson et al. 1981; Horak and Lebreton 1998). However, it is thought that a lower quality of food in urban environments may cause poorer breeding performance in some passerines (Chamberlain et al. 2009), and this may be true for raptors. For example, some species have been found to have a reduced body mass in urban environments (Liker et al. 2008; Dulisz et al. 2016; Sprau et al. 2016), thus reducing food quality for raptors. Indeed, the disease infection rate of some urban raptors is thought to be higher due to feeding largely on Feral Pigeons and other pigeon and dove species that are hosts to certain diseases, reducing nestling survival (Boal and Mannan 1999; Krone et al. 2005). Interestingly, not all species that had higher clutch sizes, brood sizes or number to fledge in urban environments had a higher nest success than rural birds. Notably, Cooper's Hawks fledged 2.25 more chicks in urban sites, but were more successful overall (i.e. produced at least one young to fledge) in rural areas. It was thought that the threat of disease caused high failures in the urban sites, with trichomoniasis causing mortality in 79.9% of urban deaths (Boal and Mannan 1999). Similarly, Tella et al. (1996) found that 4% of urban Lesser Kestrel nestlings died from disease, opposed to 2.63% of rural nestlings.

Therefore, although prey availability may be high, and nesting sites available, threats do still exist in urban environments. Collisions with vehicles and buildings is the leading cause of mortality in some urban-living raptors (Hager 2009), and human disturbance, whether accidental or not, is higher in urban environments, limiting breeding performance of some species (Berardelli et al. 2010). For example, Charter et al. (2007) found that human

disturbance (removal of nests, opening and closing windows close to nests, and watering flower pots occupied by nesting kestrels) was the cause of 41% of urban nest failures. This is reflected in the finding that, in general, brood sizes were larger in urban habitats (Figs. 3, 6), yet the number to fledge was lower (Figs. 4, 6).

Foraging guild

This review suggests that the effects of urbanisation on raptors are likely to be strongly dependent on feeding guild. Species that feed on small mammals tended to be less successful than those that feed on birds (Fig. 7b) and had lower clutch and brood sizes in urban habitats. In Lesser Kestrels, the lack of success was largely due to nestling starvation (Tella et al. 1996), and in Eurasian Kestrels urban birds tended to have a more bird-based diet, suggesting that their preferred prey were relatively scarce (Sumasgutner et al. 2014b). The importance of prey abundance for the breeding performance of small mammal-eating birds has been described in various raptor species (e.g. Korpimäki and Hakkarainen 1990; Korpimäki and Norrdahl 1991; Salamolard et al. 2000; Sundell et al. 2004). If small mammals are consistently scarce in urban environments, this may reduce the breeding performance of species that rely on them as a food resource. Indeed, small mammal abundance has been shown to differ between environments (Solonen and Ursin 2008; Solonen 2014) and the abundance of some native small mammal species has been shown to be negatively affected by urbanisation, in part due to predation pressure from Domestic Cats (*Felis catus*) and habitat fragmentation (Baker et al. 2003). Indeed, Salvati et al. (2002) found that the diet of Barn Owls in urban habitats consisted of significantly fewer rodent and shrew species than those in rural habitats. Nevertheless, the lack of fluctuation in small mammal abundance in urban areas, as is typically seen in natural environments, may actually be beneficial to small mammal-eating raptors by offering a consistent prey base (e.g. Solonen and Ursin 2008).

For some species, prey availability and quality may be high in urban environments. For instance, species that feed on birds were found to have a higher clutch size, brood size, or number to fledge at urban sites (Boal and Mannan 1999; Solonen 2008; Gahbauer et al. 2015; Lin et al. 2015; Kettel et al. unpublished). Many authors have described high abundances of birds in the urban core, including passerine species (Blair 1996; Marzluff 2001; McKinney 2006; Tratalos et al. 2007) which raptors may predate on. This may explain the increased success of some bird-eating raptor species in urban environments (Boal and Mannan 1999; Lin et al. 2015).

Management implications and future research efforts

Despite a growing interest in urban ecology, there is a lack of studies that have directly compared the breeding performance of urban and rural-living raptors. This may partly be due to the difficulty in accessing raptors nests, which are typically in inaccessible locations (Newton 1979). Critically, sample sizes in most of the studies were low and thus may have led to low statistical power. Consequently, there is a need for more research in urban raptor ecology, particularly in areas of the developing world outside the USA and Europe, and on a larger number of species.

Notably, few studies attempted to address why breeding performance differs between environments. Measuring the availability of prey and nest sites, and potential persecution and predation threats, may aid our understanding of why differences may exist and how to mitigate for negative effects. As significant effects were only found in a small number of studies, and findings from different geographical locations on the same study species often revealed dissimilar responses, repeated studies on the same species, and in different locations, may be beneficial to provide more representative results across populations. Moreover, more studies on migratory species would be beneficial to our understanding as they may respond differently to urbanisation. The year-round abundance of food and higher temperatures in urban environments may trigger earlier nesting in resident birds, but not in those that migrate to cities to breed.

It is important to understand why some species are nesting in urban areas, despite lowered breeding performance. For instance, Sumasgutner et al. (2014b) show that although Eurasian Kestrels nest in high densities in the city of Vienna, the breeding performance is lower in the urban core. It is suggested that the kestrels are attracted to the urban habitat due to the availability of nesting sites, but the quality of the habitat is overestimated (Sumasgutner et al. 2014b). Therefore, attracting raptors to urban areas should be approached with consideration of other factors important for their breeding performance. For example, providing nest boxes to attract raptors that feed on small mammals should be assessed with caution in light of the findings presented here, to avoid the risk of creating ecological traps for those species at risk.

Disturbance of nests is thought to cause failures of nesting attempts (e.g. Charter et al. 2007; Berardelli et al. 2010; Suri et al. 2017); educating the public and thus limiting the effects of their actions is therefore desirable. Encouraging quieter vehicles on roads may also benefit some species that are affected by the noise pollution of cities (Strasser and Heath 2013). Buffer zones around nests (i.e. areas where humans are encouraged not to approach)

are a possibility where sensitive species are concerned. For instance, Millsap and Bear (2000) found that Burrowing Owls fledged more young in locations that had a buffer zone of 10 m or more around the nest, protecting them from human disturbance.

Monitoring the movements and dispersal of raptors in urban environments will provide a deeper insight into the use of these habitats, which is important for aiding management and conservation efforts. For instance, Morrison et al. (2016) monitored the movements of urban-nesting Red-tailed Hawks through the use of radio telemetry and found that green spaces, such as cemeteries and parks, were valuable hunting habitats within the urban landscape. An increased understanding of the behaviour of raptors in urban environments will ultimately aid our understanding of their responses to changing environments.

Conclusion

The negative impacts of urbanisation can be vast, causing population declines in many species (Marzluff and Ewing 2001; Gaston 2010; Gil and Brumm 2014). However, the way that species respond to urbanisation is not uniform and may depend on nesting requirements, feeding ecology and vulnerability to disturbance. The findings presented in this review show that the breeding performance of some raptors is greater in urban environments (e.g. Bloom and McCrary 1996; Parker 1996; Gahbauer et al. 2015; Kettel et al. unpublished data), whilst in other species it is reduced (e.g. Tella et al. 1996; Conway et al. 2006; Charter et al. 2007). Raptors that succeed in urban areas are thought to benefit from high prey abundance (e.g. birds; Boal and Mannan 1999; Solonen 2014; Gahbauer et al. 2015; Lin et al. 2015) and reduced predation and persecution (Tella et al. 1996; Chace and Walsh 2006; Lin et al. 2015), offering them superior-quality habitat compared to that found in natural areas (Chace and Walsh 2006). Raptors that were found to be less successful in urban areas, however, are thought to be faced with a number of limitations including a reduced food supply [e.g. small mammals (Charter et al. 2007; Sumasgutner et al. 2014b)] and increased human disturbance (Charter et al. 2007; Berardelli et al. 2010). Specifically, bird-eating raptors such as Peregrine Falcons appear to be positively affected by urbanisation, whilst those that feed on small mammals, such as Eurasian Kestrels, do less well in urban environments. As different species respond in diverse ways, the importance of studying the breeding performance of raptors in urban environments on a species-by-species basis is stressed. Ultimately, the drivers altering the breeding performance of raptors are of concern in order for suitable management and conservation strategies to be implemented.

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Compliance with ethical standards

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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