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A review of survival estimates for raptors and owls

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This paper reviews the literature on survival estimates for different species of raptors and owls, examines the methods used to obtain the estimates, and draws out some general patterns arising. Estimating survival usually involves the marking of birds so that they can be recognised as individuals on subsequent encounters. Annual survival can then be estimated from: (1) birds ringed at known age (usually as nestlings) and subsequently reported by members of the public (usually as found dead), the ratio of recoveries at different ages being used to calculate annual survival; (2) marked breeding adults, trapped or re-sighted in subsequent years in particular study areas, with the proportion re-trapped (or re-sighted) in each year being taken as the minimum annual survival; (3) the same, but with the application of capture-mark-recapture (or re-sighting) methods to estimate annual survival; (4) a combination of reports of known-age dead birds and re-trapping/re-sighting of live birds, (5) use of radio- or satellite-tracking to follow the fates of individuals; and (6) the integration of these methods with other information, such as change in numbers between years, to derive estimates of survival and other demographic parameters. Studies confined to particular areas

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usually give estimates of ‘apparent annual survival’, because they take no account of birds that leave the area. However, radio- or satellite-tracking makes it possible to estimate true survival, including for pre-breeders that have low natal-site fidelity (this usually requires satellite telemetry). As in other birds, the preferred method for estimating survival has changed over time, as new and more robust methods of estimation have been developed. Methods 1-2 were the first to be developed, but without statistical under-pinning, while 3-6 were developed later on the basis of formal statistical models. This difference has to be borne in mind in comparing older with newer estimates for particular species. Published survival estimates were found for three species of Cathartidae, one of Pandionidae, 29 Accipitridae, 12 Falconidae, one Tytonidae and nine Strigidae, almost all from northern hemisphere, temperate species. In most of these species more than one estimate was available, and in some separate estimates for different age or sex groups. The main patterns to emerge included: (1) a significant tendency for annual adult survival to increase with body weight, smaller species having annual survival rates mainly of 60-70%, medium sized species mainly in the range 70-90% and the largest of more than 90%, in the absence of obvious human-caused losses; (2) a lower survival in the first or pre-breeding years of life than in subsequent years; (3) a lack of obvious or consistent differences in survival between the sexes, where these could be distinguished; and (4) in the few species for which enough data were available, a decline in annual survival rates in the later years of life.

Keywords: Birds of prey, bird ringing, capture-mark-recapture, demography, mortality, radio-tracking, survival estimation methods

The study of raptors has contributed substantially to our knowledge of basic and applied ecology, knowledge that can be transferred to many other species of birds and mammals (Newton 1979). As top predators, raptors can perform an important ecological role in limiting some prey populations, and their own numbers are in turn often influenced by the numbers of their prey (Newton 1979, 2013). Additionally, raptors require a variety of habitats for breeding and hunting, and serve as important biological indicators of the state of ecosystems (Sergio *et al.* 2005, 2006, 2008), for example with respect to chemical contamination (Ratcliffe 1970, 1993, Newton 1974, 1986, Newton & Wyllie 1992). Although some of the best examples of successful single species conservation programmes involve raptors (Cade *et al.* 1988, Newton & Wyllie 1992, Bretagnolle *et al.* 2008, Sulawa *et al.* 2010), the ecological processes influencing survival and other demographic rates for most species remain poorly understood.

Compared to many other birds, raptors generally occur at low densities, so sample-size problems are often difficult to avoid (Newton 1979). Furthermore, many species place their nests in sites that are difficult to access, which in turn makes adults hard to catch; consequently, marking of both nestlings and breeding adults in sufficient numbers requires a substantial investment of time, money and effort.

The growth rate of many raptor populations is proportionately more sensitive to adult survival rates than it is to reproductive parameters (Mertz 1971, Stahl & Oli 2006, Sergio *et al.* 2011). This means that identifying factors and processes that affect age- or life-stage specific survival rates is important for understanding raptor population dynamics. Typically, estimation of survival requires marking animals so that they can be individually identified and their fates monitored over time (Lebreton *et al.* 1992, Williams *et al.* 2002). Whatever method is used for marking, assumptions are that the marking method itself does not influence the survival of the individuals concerned, and that these individuals are representative of their population. For raptors, marking methods have included metal or coloured plastic rings, wing-tags, radio-tags and Passive Integrated Transponder (PIT) tags; while analytical methods have included models based on ring recoveries, capture-mark-recapture (or re-sight), age-composition (e.g. of museum specimens or samples of dead birds), combinations of live-recaptures and dead-recoveries (Brownie *et al.* 1985, Pollock *et al.* 1989, Lebreton *et al.* 1992, Burnham 1993, Conn *et al.* 2004, Skalski *et al.* 2005) and, more recently, integrated population models (Besbeas *et al.* 2002, Schaub & Abadi 2011). Monitoring and statistical methods to estimate survival from various data types have evolved over time, potentially affecting the accuracy and precision of survival estimates (Clobert & Lebreton 1991, Williams *et al.* 2002, Craig *et al.* 2004, Nasution *et al.* 2004).

We review the literature on survival estimates for different species of raptors and owls, discuss the methods used to obtain the estimates, and identify some general patterns arising. Study species were drawn from the families Cathartidae, Pandionidae, Accipitridae, Falconidae, Tytonidae and Strigidae, and sources searched for information included papers, technical reports, books and book chapters published over seven decades (1946-2015) that gave survival estimates of raptors and owls.

METHODS

Methods used to find relevant literature

To locate relevant publications, we searched Web of Science (<http://apps.webofknowledge.com/>) and Google Scholar (<https://scholar.google.com/>), using a combination of key words (survival, demography, population ecology, population dynamics, owl, raptor), and common and scientific names of different species. We also searched books and theses in the English language with titles suggesting that raptor survival may have been reported. Finally, we examined the references listed in those publications that had not been found in other ways. However, we cannot claim to have found every relevant publication in English, and for various reasons (such as small or obviously biased samples) some of those found are not included in this review.

Methods used to estimate survival

The methods used for survival estimation in birds have changed over time as different approaches have been developed and more sophisticated models have become available. The main methods are listed below, in approximate order of their development, and their strengths and limitations are discussed (Table 1). Methods 1 and 2 were the first to be used and can be classed as informal in that they lack statistical underpinning, whereas the later-developed methods 3-6 are all based on formal statistical models (as are later modifications of method 1).

1. Informal methods based on ring-recovery data from dead birds

Ring recovery data come from birds that have been marked (for raptors, typically as nestlings), released and subsequently found and reported dead, usually by members of the public. Under this sampling method, birds are normally encountered only once after ringing. In some countries, many species of birds, including raptors, have been ringed over many years, and databases of their initial marking and subsequent recovery have been maintained by national organizations (e.g. British Trust for Ornithology [BTO, <http://www.bto.org>] in the UK, United States Geological Survey [USGS, <http://www.usgs.gov>] Bird Banding Lab in the USA). Data from ring recovery studies allow estimates of survival probabilities and other parameters among birds of different sex and age classes, regardless of their dispersal distances, and may also provide information on causes of death (Newton 1979).

Estimating survival based on dead recoveries entails comparing, for a given cohort of nestlings, the number recovered dead in each year after ringing to give a 'static life table'.

The rate at which recoveries decline with time since ringing reflects mortality. Usually, the samples for particular years are small, so the data for multiple years are pooled, and treated as a single cohort. Any time trends in survival and recovery parameters are thereby masked.

Many estimates of survival have been made for raptors and other birds by this 'age ratio method', assuming no significant variation in survival or reporting rates over time or between age and sex groups, and no loss of rings during the lives of the birds (e.g. Haukioja & Haukioja 1970, Anderson *et al.* 1985, Newton & Rothery 1997). However, these assumptions are often rejected when tested, including in studies of raptors (Anderson *et al.* 1985). For these and other reasons, more statistically robust ring recovery models (e.g. Brownie *et al.* 1985) were developed to estimate bird survival, and their use for raptors has increased in recent years (Francis & Saurola 2002, Sulawa *et al.* 2010) (Supporting Online Table S1).

When used either with appropriate models or in conjunction with live-encounter (CMR) data, ring-recovery data offer opportunities to estimate true survival (see below), and to examine trends in survival over time.

2. Informal methods based on live encounters

These methods are based on re-trapping or re-sighting the same marked individuals, usually at nest sites, in the same study area in successive years. Minimum annual survival is estimated from the proportion of marked territorial birds present in one year that were also found to be present in a subsequent year – the 'return rate', or its complement 'turnover' (Newton 1979, Newton *et al.* 1983, Sandercock 2006, Hernández-Matías *et al.* 2011). The method does not distinguish between death and emigration, nor does it adequately account for detection (or recovery) probabilities that are <1 and vary over time during the study (Sandercock 2006). Survival estimates based on this method may, however, be acceptable for species that show high site fidelity and in which all (or almost all) individuals still in the study area can be detected each year. It has been used to estimate survival in Peregrine Falcons (Newton & Mearns 1988, Tordoff & Redig 1997), Eurasian Sparrowhawks *Accipiter nisus* (Newton & Rothery 1997) and various eagle species (Green *et al.* 1996, Carrete *et al.* 2002, Hernández-Matías *et al.* 2011), among others (Table S1).

This method of regular sampling can be challenging for species in which individuals are difficult to capture. Some of these challenges have been partially addressed by: (1) marking nestlings, or trapping and marking adults, in a way that they can be identified later without recatching them (e.g. Craig & Enderson 2004, Cadahía *et al.* 2005, Rosenfield *et al.* 2009); some recent studies have used PIT tags, allowing the ‘electronic recapture’ of birds at nests (Smith *et al.* 2015); (2) using non-invasive methods such as moulted feather patterns or DNA extracted from feathers found at nests to identify individuals (Newton 1986, Wink *et al.* 1999, Rudnick *et al.* 2005, Kenward & Katzner 2007); or (3) using individual recognition through plumage features (Hernández-Matías *et al.* 2011).

Annual adult survival has also been estimated in other ways from this type of data. In a breeding population (where breeding necessitates territory occupancy) with zero population growth, annual adult mortality is equal to the annual recruitment of new adults into the breeding population (Newton 1979, Newton & Mearns 1988). If all adults in the breeding population in previous years have been marked, so that, in any one year, they can be distinguished from new recruits, the proportion that new recruits form of the total breeders in that year reflects the annual mortality of established breeders. Once a study has continued long enough for all individuals to be of known age, the ratio of each age group to the next can be used to estimate the average annual survival, as in method 1 above.

3. Methods based on Capture-Mark-Recapture (CMR)

Like Method 2, CMR studies involve capturing, marking and releasing individuals over time, and keeping track of marked individuals so that an individual capture history can be constructed. The main difference is that formal statistical models are used to analyse the resulting data. For territorial raptor populations, multistate CMR models provide a flexible means of dealing with the related age-specific phenomena of survival and recruitment to a breeding population (Williams *et al.* 2002). Specifically, birds ringed as nestlings may have no chance of being detected (re-sighted) until they join the territorial breeding population, leading to biased estimates based on standard age-specific CMR models. More generally, individuals of the same age may have both different detection probabilities and different survival rates according to whether or not they have acquired a nesting territory, the latter birds often being termed ‘floaters’. An appropriate multistate model structure for birds ringed as nestlings in these situations considers a pre-recruitment state with detection probability fixed to zero, together with age-specific recruitment probabilities reflecting the likelihood

that a pre-recruit will enter the breeding population and thereafter be subject to breeder detection probabilities. In this way, CMR models provide a means of dealing with floaters.

These open population CMR models have been used to estimate survival of raptors, permitting gains from births and immigration, and losses from deaths and permanent emigration to be estimated between sampling occasions (Gould & Fuller 1995, Brown *et al.* 2006, Steenhof *et al.* 2006, Faccio *et al.* 2011, Altwegg *et al.* 2014). Examples are given in Tables 2 and S1.

Like Method 2 above, CMR-based approaches have limited use for estimating survival probabilities of species that show low site fidelity (i.e. when dispersal distances are long relative to the size of the study area), or for dispersing sex and age classes (Sandercock 2006), in which permanent emigration is a major cause of the disappearance of birds from a study area. However, open population CMR models can be used together with radio-tracking data to estimate true survival, or with ring-recovery or other ancillary data to estimate true survival and other population parameters (see below) (Burnham 1993, Williams *et al.* 2002, Kendall *et al.* 2006).

4. Formal methods based on joint live encounters and ring recoveries

Studies involving a combination of live encounters and ring recoveries also involve the capture, marking and release of individuals. Subsequent live-encounters usually derive from the area of initial release, but ring recoveries can come from a much larger geographical region, providing information on permanent emigration (Burnham 1993, Barker 1997, Williams *et al.* 2002). The main advantage of combining live encounter and dead recovery models is that apparent survival can be decomposed into the probabilities of true survival and site fidelity (to the area in which live encounters are made) (Burnham 1993, Barker 1997, Williams *et al.* 2002). Additionally, joint models can be used to test explicitly for the effects of age, sex, and environmental conditions on site fidelity and true survival.

Statistical models for joint analysis of live-encounter and dead-recovery data to estimate survival are well developed (Table 1), but have been used rarely on raptors, except for Peregrine Falcons *Falco peregrinus* (e.g. Kauffman *et al.* 2003, Craig & Enderson 2004, Smith *et al.* 2015) (Table S1).

5. Formal methods based on tracking data

Radio-tracking studies involve capturing birds, fitting them with tags, and monitoring their fates (Kenward 1987). Tracking devices can be ‘conventional’ (VHF, UHF) or satellite-based (e.g. Argos, GPS or Globalstar) (Fuller *et al.* 2005). Radio-tagging is one of the best methods for monitoring the fates of individuals because, using this method, all tagged birds can be detected with near-certainty if they are present within the search area, and their fates determined unambiguously. Using satellite-received tags, the fates of many individuals can be monitored simultaneously wherever in the world they travel (Bowman *et al.* 1995, Whitfield *et al.* 2004, McIntyre 2005). Technical advances through time have made radio-tracking more flexible and increasingly reliable in application.

Use of radio-tags sometimes allows researchers better to distinguish between losses attributed to death and permanent emigration, and hence to estimate true survival as opposed to apparent survival (the combination of mortality and permanent emigration) (Kenward 1999, Williams *et al.* 2002, Fuller *et al.* 2005), as well as to identify the cause of mortality when dead animals can be retrieved (Heisey & Patterson 2006). Radio-tracking data can also be used in conjunction with other data types (see below) to estimate survival rates from capture-recapture data. Consequently, statistical models have been developed to use both live-encounter and radio-tracking data to estimate true survival (Powell *et al.* 2000, Nasution *et al.* 2004).

Tracking data have provided estimates of survival in large raptors, such as eagles (Ferrer & Calderón 1990, Bowman *et al.* 1995, Harmata *et al.* 1999, Hunt 2002, McIntyre 2005) and hawks (Zelenak *et al.* 1997, Kenward 1999), that are difficult to monitor using other methods (Table S1). Tracking also provides the most reliable way to estimate juvenile (first-year) survival in species with low natal-site fidelity, or age-class survival among pre-breeders of long-lived species with delayed maturity (Ferrer & Calderón 1990, Bowman *et al.* 1995, Kenward 1999, Mannan & Matter 2004, McIntyre 2005, Davies & Restani 2006) (Table S1).

Set against these advantages, tracking studies can be prohibitively costly due to the expense of deploying sufficient numbers of tags and monitoring the individuals concerned. There can also be problems caused by the short life-spans of most transmitters, possible reduction in survival associated with the transmitters (Steenhof *et al.* 2005), and the effects of right-censoring when fate and censoring are not independent events (Bennetts *et al.* 1999, Williams

et al. 2002, Zens & Peart 2003). An additional difficulty arises when mortality cannot be distinguished from transmitter failure, a situation more likely in studies that track wide-ranging species via satellites. Signals that become irregular before stopping altogether are usually taken to signify tag failure, but signal characteristics and onboard sensors of some satellite tags can suggest whether a tag has failed, become detached or its carrier has died. Such tags are therefore especially useful in the study of survival.

6. *Integrated Population Models*

These models provide a framework that can use multiple types of data (typically, time series of abundance, productivity, and CMR and/or tag recovery data) to estimate demographic parameters and make statistical inferences about these parameters (Besbeas *et al.* 2002, Schaub & Abadi 2011, Kéry & Schaub 2012, Tenan *et al.* 2012). Developing integrated population models involves three steps (Schaub & Abadi 2011, Kéry & Schaub 2012): (1) the development of a model that links multiple data types that pertain to the same demographic process(es); (2) development of likelihoods for individual datasets; and (3) integration of these likelihoods to form a joint likelihood for all data types, permitting estimation of relevant parameters and statistical inferences using either frequentist or Bayesian analytical frameworks.

The advantages of integrated population models include: (1) the combination of information contained in several separate datasets, so that parameters estimated using this approach are generally more precise and statistical inference is stronger than would be possible using independent analyses of individual datasets; (2) the estimation of more demographic parameters than would be possible if each dataset were analysed separately; and (3) the direct estimation of standard errors (or credible intervals) for all estimable parameters (Besbeas *et al.* 2002, Schaub & Abadi 2011, Kéry & Schaub 2012). So far, integrated population models have been used to estimate survival probabilities (and other demographic parameters) among raptors for Eurasian Eagle Owl *Bubo bubo*, California Spotted Owl *Strix o. occidentalis* and Red Kite *Milvus milvus* (Schaub *et al.* 2010, Tenan *et al.* 2012, Tempel *et al.* 2014).

Methods used to examine survival in relation to body mass and sex in different species

To estimate survival in relation to body mass for different species, we used only data for adult birds explicitly obtained by the statistically formalised methods 3-6 above, thus excluding estimates from methods 1-2 which were most open to bias. Where separate

estimates were available for the sexes, we used gender-specific masses; where estimates were for males and females combined, or where the sexes of the birds in the study were not known, we used the arithmetic mean of the male and female masses. Where separate estimates were available for different years in the same study of a species or when estimates were made for different ages of adult birds, we took the geometric mean of those estimates. Where estimates were available for different areas or circumstances in the same study, we used separate estimates for each area or circumstance (e. g. low versus high prey abundance, one habitat versus another). This meant that variable numbers of estimates were available for different species, which we allowed for statistically by treating species as a random effect in linear mixed effect models (Zuur *et al.* 2009). All estimates used to calculate relationships between survival and body mass or sex are given in Table 2, and the full data are summarised in Table S1. Table 2 lists 45 published survival estimates for 30 species of diurnal raptors, and 23 for nine species of owls. Table S1 lists survival estimates of 45 species of diurnal raptors from 130 publications, and ten species of owl from 29 sources.

RESULTS

Species studied and constraints in data

We found survival estimates for three species of Cathartidae, one of Pandionidae, 29 of Accipitridae, 12 of Falconidae, one of Tytonidae and nine of Strigidae (Table S1). In most of these species, more than one estimate was available from different areas or time periods. Almost all of the 159 studies were from the temperate region of the northern hemisphere. Most attention has been directed to species that suffered severe population declines or were considered threatened or endangered for other reasons (e.g. Newton 1986, Ratcliffe 1993, Anthony *et al.* 2006, Forsman *et al.* 2011, Ganey *et al.* 2014).

Among these studies, some reported sex-, age-, region- or time-specific variation in survival (Newton & Rothery 1997, Newton *et al.* 1997, Martin *et al.* 2006, Karell *et al.* 2009, Forsman *et al.* 2011, Ganey *et al.* 2014), while others simply provided estimates of overall, or pre-breeder and breeder survival (Table S1). Owing to difficulties of recapturing, re-sighting or tracking birds until they become breeding adults, and the limited use of the relatively new statistical models developed to deal with such difficulties, estimates of juvenile and pre-breeding survival were fewer, more variable and probably less reliable than estimates of adult survival, especially for species with delayed maturity (see below). Furthermore, some of the

studies listed in Table S1 refer to populations in which survival rates were lower than expected because of human behaviour of one form or another: for example, lead poisoning of California Condors *Gymnogyps californianus* or direct persecution of Hen Harriers *Circus cyaneus* (Etheridge *et al.* 1997, Meretsky *et al.* 2000). These were obvious cases, but many other studies, especially in the early years, may have involved populations subject to human killing. Despite some variability and inconsistencies among estimates, some general patterns in the survival rates of raptors and owls were evident.

Body-size and survival

In line with well-established allometric relationships (Calder 1984, Gaillard *et al.* 1989, Charnov 1993, Dobson & Jouventin 2010), adult survival among different raptor species was positively related to log-transformed adult body mass in both diurnal raptors and owls (Fig. 1), although with much additional variation within and between species. Analysis of covariance with species as a random effect in a linear mixed model (implemented using R package *nlme*; Pinheiro *et al.* 2014) provided no evidence of different slopes for diurnal raptors and owls ($t = 0.806$, $P = 0.422$). In populations largely free of human-induced mortality, small species, such as Eurasian Sparrowhawk and Common Kestrel *Falco tinnunculus*, typically showed annual adult survival rates of around 60-70%, while medium sized falcons and hawks showed adult survival rates around 80-90%, and large eagles and vultures of more than 90%, although exceptions occurred among the estimates for all three groups (Tables 2, S1).

Age differences in survival

It would be expected that young birds, because of their inexperience and low social status, would survive less well than older individuals. Most studies reporting age-specific estimates indicated that annual survival rates of juveniles or sub-adults were substantially lower than those of adults of the same species (for exceptions see Bowman *et al.* 1995 for Bald Eagle *Haliaeetus leucocephalus*, Sulawa *et al.* 2010 for White-tailed Eagle *H. albicilla*).

Furthermore, in studies in which adult age-classes were distinguished, survival of the very oldest age groups among breeders tended to decline, presumably reflecting senescence or relegation to floater status (e. g. Newton *et al.* 1997, Sergio *et al.* 2011, Tenan *et al.* 2012, Ganey *et al.* 2014). In populations of long-lived eagles, in which competition for places in the breeding population is often high, mortality rates amongst late-aged sub-adults may also be high (e. g. Saurola *et al.* 2003), a situation attributed to aggressive interactions between

territory seekers and territory holders (Haller 1996, Sulawa *et al.* 2010). Such competition may result in some adults being killed, but the effect on the overall rate of adult mortality may be less obvious if it disproportionately affects senescent birds. Evans *et al.* (2009) found no increase in mortality in White-tailed Eagles as they approached adulthood in an environment in which potential but unoccupied breeding habitat was abundantly available, although adults survived generally better than non-adults.

The degree of difference in estimated survival between juvenile and adult raptors depends largely on estimation method (Table S1). Because juveniles disperse in greater proportion and over longer distances than adults, any method based on a confined study area that does not distinguish between death and emigration leads to under-estimation of juvenile survival, and enhances the difference in estimated survival between juveniles and adults. In theory, ring recoveries could provide reliable estimates of survival in different age groups, including first-year birds, but it has long been suspected that dead first-year birds are more likely to fall into human hands than dead older birds, which based on Method 1 would overestimate first-year mortality (Newton 1979, Frances & Saurola 2002). Juveniles are more likely to be shot or trapped, or to venture near human habitation. For these reasons, estimates for juveniles based on radio-tracking are probably the most reliable available, providing that the tags do not affect survival, that right censoring is independent of bird fate, that they function properly for long enough and that attempts are made to follow each individual wherever it goes. We judge that at least four of the radio-tracking studies in Table S1 meet these criteria sufficiently well to provide reliable estimates of first-year survival. These studies gave estimates of adult and first-year survival in the Bald Eagle of 88% and 71% respectively, and in the Common Buzzard *Buteo buteo* of 88-91% and 66-73% respectively (Bowman *et al.* 1995, Kenward *et al.* 2000). In the Snail Kite *Rostrhamus sociabilis*, estimates of adult survival in three different years were given as 89%, 86% and 82%, and of juvenile survival in the same years as 67%, 45% and 44% respectively (Bennetts *et al.* 1999). In the Goshawk *Accipiter gentilis*, with an adult survival of 83% in both sexes, estimated first-year survival was 71% in females and 59% in males, the only study to separate the sexes of first year birds (Kenward *et al.* 1999). Finally, in a study of the Red Kite that used an integrated population model to provide the estimates, adult and first-year survival were calculated at 96% and 89%, respectively (Tenan *et al.* 2012). So in these various estimates, first-year survival emerged as 7-48 percentage points lower than adult survival in the same population. Other estimates in Table S1 obtained by radio-tracking refer to adult and first-year survival in different

populations of a species, so are less strictly comparable, while some of the estimates obtained by other methods could be acceptably accurate, but the methodology leaves them open to doubt.

Sex differences in survival

In raptors and owls, females are bigger than males. In most species this difference is small, but in others females can weigh up to twice as much as males (Newton 1979). Particular interest therefore attaches to any sex differences in survival, and on the basis of weight, females would be expected to show higher annual survival rates than males. For 32 comparisons involving seven species of diurnal raptors and four species of owls listed in Table S1, separate survival estimates with standard errors were available for adults of both sexes. In most of these comparisons, the estimates for each sex varied by no more than a few percentage points, and either males or females could show higher survival. However, differences exceeding five percentage points were found in 12 comparisons. In diurnal raptors these large differences were in highly dimorphic species, but they were not consistent within species (see the different estimates for Peregrine Falcon and Eurasian Sparrowhawk in Table S1). Among owls, sex differences greater than five percentage points were found in one study of Tawny Owls *Strix aluco* (females showing higher survival), and in three studies of Burrowing Owls *Athene cunicularia* (males showing higher survival in two, females in one). Sufficient information was provided using methods 3-6 to test the statistical significance of apparent sex differences in seven studies of diurnal raptors, and in 23 studies of owls, including 16 of Spotted Owls. Only four were statistically significant (program CONTRAST; Hines & Sauer 1989): Southern Crested Caracara *Caracara plancus*: $\chi^2 = 69.230$, female 3% higher than male, $P < 0.0001$, Morrison 2003; Hen Harrier, $\chi^2 = 5.586$, female 18% higher than male, $P = 0.018$, Picozzi 1984; two of three studies of Burrowing Owl, $\chi^2 = 4.5$, male 12% higher than female, $P = 0.034$, Millsap 2002; $\chi^2 = 15.56$, male 23% higher than female, $P = 0.0001$, Wellicome *et al.* 2014).

Finally, we tested the relationship between the ratios of female:male survival and body mass. With species included as a random effect, no evidence of a relationship emerged, either for diurnal raptors alone ($t = -1.536$, $P = 0.199$), owls alone ($t = 1.240$, $P = 0.341$) or both groups combined ($t = -0.647$, $P = 0.524$). Sex differences in survival of owls and raptors might be expected for reasons other than body size: for example, human persecution (in which females suffer higher mortality because they are more easily killed at the nest), and differential

migration (in which the sexes winter in partly different regions imposing different mortality rates). In view of these findings and possibilities, we conclude that the data provide no convincing or consistent evidence for differential survival between the sexes of adult raptors and owls linked to size dimorphism.

Possible methodological differences in survival estimates

Examination of survival rates of Eurasian Sparrowhawks and Peregrine Falcons studied in different time periods hinted that survival rate estimates may often have been lower in earlier than in later periods. This apparent temporal trend was not statistically significant in either species, and could in any case be influenced by change in estimation methods. Nevertheless, a change in survival over the years could have been expected in response to legal protection and banning of organochlorine pesticides, as the various survival estimates for these species spanned the period before and after these events (e.g. Newton 1986, Cade *et al.* 1988, Wyllie & Newton 1991, Newton & Wyllie 1992).

It is accepted that estimation methods alone can cause substantial variation in survival estimates (Clobert & Lebreton 1991). For example, Francis and Saurola (2002) compared estimates of age-specific survival among Tawny Owls from the same population using formal estimation approaches based on alternative data types: (1) recoveries of birds ringed as nestlings; (2) recoveries of birds tagged as juveniles and adults; (3) recaptures of birds tagged as juveniles; (4) recaptures of birds tagged as juveniles and adults; (5) recoveries and recaptures of birds tagged as juveniles; and (6) recoveries and recaptures of birds tagged as juveniles and adults. Depending on the data type and analytical method, estimated survival of first-year birds ranged from 10.1% to 47.8%, while that for adults was effectively the same at 69.9-72.2%. First-year survival based on recoveries of birds ringed as nestlings was biased high because of violation of the assumption of age-independent recovery rates: juveniles were recovered disproportionately more often than older birds. Differences in survival caused primarily by estimation method or data type have also been reported for the Peregrine Falcon (Gould & Fuller 1995), Eurasian Sparrowhawk (Newton 1986), Bonelli's Eagle *Aquila fasciata* (Hernández-Matías *et al.* 2011), Snail Kite (Bennetts *et al.* 1999) and Red Kite (Tenan *et al.* 2012).

DISCUSSION

Apparent survival versus true survival

In studies based on specific study areas, most published estimates of survival also include permanent emigration. In effect, they estimate the product of true survival and site fidelity. The degree to which true and apparent survival in adults differs depends on the proportion of adults that leave the area, and in some species, such as Peregrine Falcon and Bald Eagle, this proportion seems so low that apparent survival could closely approximate true survival. Although estimating true survival is desirable, it may be sufficient to estimate apparent survival when comparing rates among different groups of birds of the same species (treatments, management options, habitats, or other factors), if permanent emigration is similar among the groups being compared. For studies directed at changes in abundance on a study area, it may not be necessary to split losses into deaths versus emigration, or gains into local reproduction versus immigration (see Appendix 3 of Franklin *et al.* 2004). However, true survival estimates are required when the objective is to test life-history theory based on comparative studies, to estimate population growth rates using projection matrix approaches or to develop recovery plans for imperilled species. In all these cases, assessment of population status, or population growth rate based on apparent survival without appropriately accounting for immigration may result in misleading conclusions (e.g. Cooch *et al.* 2001, Gerber 2005). In particular, it is common practice to assess the conservation status of species by computing asymptotic population growth rates using population projection matrices (e.g. Caswell 2001). When such matrices use apparent survival, then population losses include movement, while the recruitment information used in such matrices typically includes reproduction (clutch size, nest success, etc.), but not immigration. Such matrices are therefore asymmetric with respect to movements, typically including movement in estimates of losses (emigration) but not in estimates of gains (immigration), and thereby leading to underestimates of projected growth rates (e.g. Nichols & Hines 2002). This is a methodological deficiency which is by no means specific to raptors and owls.

Demographic analyses of, for example, Spotted Owls (e. g. Franklin *et al.* 2004, Forsman *et al.* 2011) use CMR methods (e.g. Pradel 1996) at specific study sites to estimate realized (as contrasted with asymptotic) population growth rates directly. These growth rates estimate changes in numbers of birds on specific study sites, with losses including both permanent emigration and death, and gains including recruitment from both local reproduction and

immigration. These growth rates are symmetric with respect to movement and are intended to reflect true changes in numbers in the landscape, rather than theoretical changes that would occur if there were no movement.

The question of whether variation in survival detected in comparative analyses reflects true variation in survival or variation in methodology is also relevant to many other groups of birds. Historically, investigations of waterfowl were among the first to use probabilistic methods that considered the detection process (e.g. Johnson *et al.* 1992). Critiques such as those of Clobert and Lebreton (1991) and Boulinier *et al.* (1997) led to accelerating adoption of CMR methods for survival studies of birds. Some studies of raptors provide examples of cutting-edge research in demography and population dynamics. Examples include studies on the Spotted Owl (e.g., Blakesley *et al.* 2010, Forsman *et al.* 2011, Ganey *et al.* 2014), Red Kite (Tavecchia *et al.* 2012, Tenan *et al.* 2012) and Eagle Owl (Schaub *et al.* 2010).

Although raptors are generally rarer than many other birds, study of this group has contributed substantially to our understanding of avian population dynamics, in part because many raptor species are relatively conspicuous and long-lived, and can carry large visual identification marks or transmitters. They are also highly territorial which, together with site fidelity in most species, gives high re-encounter rates.

Territorial breeders and floating non-breeders

Estimates of adult survival in raptors are mostly based on breeding birds, and so do not include floating (non-breeding) adults. This is true of many other birds, including some that move from breeder to floater status in different years in response to factors such as fluctuations in food supply. Non-breeding adults could survive better or worse than breeding adults, depending on the conditions in which they find themselves. For example, in a landscape which is filled to capacity with territorial breeding pairs, floaters may be constrained to occupy less favourable areas where their mortality rates are higher.

Alternatively, in landscapes where food is plentiful but breeding sites are limiting, floaters may be able to survive as well or better than breeders, though unable to obtain a nesting territory (e. g. Hunt *et al.* 1998, Newton 1998). In addition, survival of breeding adult raptors may be lower than that of floaters in areas where adults are often shot at the nest, a common occurrence in some species in some areas (e. g. Etheridge *et al.* 1997, Whitfield *et al.* 2004).

Continuing threats to raptors

Although raptor populations have generally recovered from the global declines caused by organochlorine pesticides during the 1950-1960's (e. g. Newton 1998, Banks *et al.* 2010), there is no shortage of new threats. Inadvertent diclofenac poisoning has caused a catastrophic collapse of populations of several species of south Asian vultures (Oaks *et al.* 2003, Green *et al.* 2006), and the toxic effects of lead ingestion have had adverse impacts on the critically endangered California Condor, the rare Steller's Sea Eagle *Haliaeetus pelagicus* and other raptors (Watson *et al.* 2009). Organophosphate insecticides have caused mass mortality of Swainson's Hawks *Buteo swainsoni* and other raptors in South America (Goldstein *et al.* 1996). Illegal poisoning or other killing affected 40% of 103 Red Kites found dead in Scotland (Smart *et al.* 2010), and was the most important recent cause of mortality of Red Kites in Spain, suppressing population growth rate by 20% (Tenan *et al.* 2012); it is also an ongoing problem in parts of Africa greatly reducing vulture numbers (Ogada *et al.* 2012, 2015). Those raptors that are predators of game birds or racing pigeons have long been subject in Britain and elsewhere to shooting, poisoning and other forms of persecution (e. g. Etheridge *et al.* 1997, Whitfield *et al.* 2004, 2008, Newton 2013). Other relatively new threats to raptors include collisions and electrocutions related to power generation and distribution (including wind turbines), and communication towers (Subramanian 2012, Tavecchia *et al.* 2012, Angelov *et al.* 2013), and the unsustainable harvest of some species in some regions for falconry (Kovács *et al.* 2014). As with previous threats, mortality due to these anthropogenic causes is often partly or entirely additive to natural mortality, and frequently leads to population declines. Those raptor species that migrate are thereby exposed to different mortality threats in different regions.

Future studies

In addition to providing data necessary to estimate survival probabilities, radio-tracking studies can provide a wealth of other information (e. g. local movements, dispersal and migration routes, space and habitat use, abundance) unattainable in other ways (Fuller *et al.* 2005). We can therefore expect that radio-tracking will continue to play an important role in raptor research. However, it is expensive, requires high investment of time and effort, and radio-transmitters can affect survival (Steenhof *et al.* 2006). In most analyses of radio-tracking data, individual birds are censored for one reason or another, and a challenge in such analyses is to ensure that censoring is independent of bird fate, as dependence can produce biased survival estimates (Bennetts *et al.* 1999).

In future, we can also expect to see an increase in the number of studies that use multiple data types, including time series of annual counts, radio-tracking, live-recaptures, mark-resighting, and dead-recoveries (from a larger area), all incorporated within a single analytical framework (Burnham 1993, Barker 1997, 1999, Williams *et al.* 2002, Nasution *et al.* 2004, Schaub *et al.* 2010, Tenan *et al.* 2012). The use of financial incentives can improve rates of ring-reporting by members of the general public in hunted species (Nichols *et al.* 1991, 1995), as can a shift from standard mail to telephone and web-based reporting (Royle & Garrettson 2005, Boomer *et al.* 2013). In addition, the use of electronic recaptures using technologies such as Passive Integrated Transponders can potentially improve recapture rates and quality of monitoring data (Barbour *et al.* 2013). Recent developments in GPS tracking technology that allow the precise location of an animal at frequent intervals, can provide data necessary for accurate and precise estimates of survival and other demographic measures, as well as pin-pointing the time and place of death (McIntyre 2012). Data sharing and collaborative initiatives (e.g. *Movebank*; Kranstauber *et al.* 2011) offer opportunities to overcome sample size limitations, extend temporal and spatial scales of inference, harness analytical skills of other researchers and potentially facilitate analyses of older data using new methods.

Future research should be driven mostly by conservation concerns, perceived challenges and available funding. However, studies on relatively common species may continue to fill gaps in understanding, while improved survival estimation procedures and advances in technology make population studies of some hitherto ‘difficult’ species feasible. Whereas species such as the Common Kestrel and Eurasian Sparrowhawk provided initial insight into raptor ecology, it is now possible to effectively study other species that, for example, are larger, longer-lived and have delayed maturity, and also to accumulate information on sex- and age-specific survival. Given the critical roles of raptors in a variety of ecosystems and their roles as indicator and flagship species, investment in raptor research that uses state-of-the-art methods to estimate mortality may be well justified.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article

Table S1. Survival estimates for diurnal raptors and owls.

FIGURE LEGEND

Figure 1. The relationship between body mass and adult survival in diurnal raptors, owls and both diurnal raptors and owls combined. See Table 2 for a detailed description of data.

Table 1. Summary of methods for estimating survival appropriate to different data types, with their pros and cons.

Method (data type)	Analytical procedures	Estimate of survival	Advantages	Disadvantages
1. Ring-recovery	Informal based on age ratios among recoveries, or formal using Seber and Brownie parameterizations of ring recovery models	True, usually. Apparent, if recovery occurs only in local areas	Less expensive than CMR or radio-tracking studies Offer a cost-effective way of monitoring raptor vital rates over the long-term	Informal models do not allow for variations of recovery and reporting rates. Models with fewest assumptions require releases or re-sightings of both adult and young birds. Adults are often difficult to catch or re-observe. Low recovery and/or reporting rates often lead to inadequate sample size
2. Observational data with and without individual identification	Informal methods: territory turnover, age ratio	Bias can be in either direction, depending on methodological details	Cheapest and easiest method to estimate survival	Several assumptions are difficult to meet, including: equal detectability for age classes; stable age distribution; stationary population

				Estimates do not distinguish between permanent emigration and death
3. Capture-Mark-Recapture or Resight (CMR)	Cormack-Jolly-Seber, multistate models	Apparent	Less costly and more efficient sampling than radio-tacking studies. Allows monitoring of a large number of individuals simultaneously	Does not distinguish between death and emigration Limited use for raptor species that exhibit low site fidelity
4. Joint live encounters – ring recoveries	Burnham and Barker models	True	Distinguish between permanent emigration and death by estimating fidelity and survival rates separately	Multiple sources of information are unlikely to be available for many species. Sample size often small
5. Radio-tracking	Kaplan-Meier, Cox Proportional Hazard or discrete time analogues, CMR models (if detection rates are <1)	Can be true – depends on whether birds leave the area, and become immune to sampling efforts	Distinguishes between death and permanent emigration Allows cause-specific mortality analysis Provides additional ecological	High financial cost and time-consuming sampling Short lifespans of most radio transmitters Possible effects of radio-tags on

			information (e.g., movement, space and resource use patterns)	survival Potential problems with non-independence of censoring and fate
6. Multiple data types (e.g., time series of counts, live encounter, ring recoveries, radio-tracking)	Integrated population models	True, usually. Apparent, if data permitting separation of loss into emigration and death are not available	Distinguishes between permanent emigration and death, given appropriate data Permit estimation of important demographic parameters, including survival and population growth rates Estimates generally more precise	Requires multiple data types, which may not available for many species Bias induced by inappropriate modelling of one parameter can translate into biases in multiple parameter estimators Requires strong statistical and programming skills

Table 2. Annual adult survival estimates (SE in parentheses when available) and body mass for 30 species of diurnal raptors and nine species of owls used to examine the relationship between body mass and adult survival. When survival was reported for males (M) or females (F), adult body mass is given for that sex. When survival is reported for both sexes (B), average male and female body mass is given for males and females. Estimation methods are described in Table 1, and body masses are from Dunning (1992, 2007). Notes indicate specific circumstances (if any) under which survival rates were estimated.

Species	Sex	Mass (g.)	Annual adult survival (SE)	Method	Reference	Notes
A. Diurnal raptors						
Andean Condor <i>Vultur gryphus</i>	B	11300	0.94	5	Temple & Wallace (1989)	
Osprey <i>Pandion haliaetus</i>	B	1505.5	0.64	5	Klaassen <i>et al.</i> (2014)	
Egyptian Vulture <i>Neophron percnopterus</i>	B	2082	0.75 (0.02)	3	Grande <i>et al.</i> (2009)	non-breeding
	B	2082	0.833 (0.022)			breeding
European Honey-buzzard <i>Pernis apivorus</i>	B	758	0.813 (0.023)*	3	Bijlsma <i>et al.</i> (2012)	multiple adult ages
Eurasian Griffon <i>Gyps fulvus</i>	B	7436	0.987 (0.006)	3	Sarrazin <i>et al.</i> (1994)	released birds

Golden Eagle <i>Aquila chrysaetos</i>	B	4263.5	0.896 (0.371)	5	Hunt <i>et al.</i> (1998)	windfarm, breeders
	B	4263.5	0.909 (0.025)		Hunt <i>et al.</i> (2002)	windfarm, breeders
Bonelli's Eagle <i>A. fasciata</i>	B	2000	0.87	3	Hernández-Matías <i>et al.</i> (2011)	
Eurasian Sparrowhawk <i>Accipiter nisus</i>	F	325	0.586 (0.103)*	3	Newton <i>et al.</i> (1997)	multiple adult ages
	F	325	0.567 (0.091)*			
	F	325	0.656 (0.089)*			
	F	325	0.574 (0.081)*			
Northern Goshawk <i>A. gentilis</i>	M	1137	0.83 (0.09)	5	Kenward (1999)	
	F	912	0.83 (0.09)			
Western Marsh Harrier <i>Circus aeruginosus</i>	B	711.5	0.56	5	Klaassen <i>et al.</i> (2014)	
Hen Harrier <i>C. cyaneus</i>	M	430	0.72 (0.07)	3	Picozzi (1984)	
	F	430	0.90 (0.03)			
	F	430	0.397	3	Etheridge <i>et al.</i> (1997)	grouse moor
	F	300	0.778			other moor
Montagu's Harrier <i>C. pygargus</i>	B	315.5	0.59	5	Klaassen <i>et al.</i> (2014)	

Red Kite <i>Milvus milvus</i>	B	1080	0.87 (0.12)	3	Smart <i>et al.</i> (2010)	wild-bred birds
	B	1080	0.85 (0.20)			released birds
	B	1080	0.77 (0.03)	3	Tavecchia <i>et al.</i> (2012)	
	B	1080	0.955	6	Tenan <i>et al.</i> (2012)	poison free
Black Kite <i>M. migrans</i>	B	567	0.789 (0.008)	3	Sergio <i>et al.</i> (2011)	
White-tailed Eagle <i>Haliaeetus albicilla</i>	B	4793	0.715 (0.046)	3	Saurola <i>et al.</i> (2003)	
	B	4793	0.966 (0.014)	3	Evans <i>et al.</i> (2009)	wild-bred birds
	B	4793	0.942 (0.022)			released birds
Bald Eagle <i>H. leucocephalus</i>	M	5350	0.86 (0.05)	5	Bowman <i>et al.</i> (1995)	
	F	4130	0.90 (0.04)			
	B	4740	0.766*	5	Harmata <i>et al.</i> (1999)	multiple adult ages
Snail Kite <i>Rostrhamus sociabilis</i>	B	420	0.861 (0.034)	3	Bennetts <i>et al.</i> (1999)	Cormack-Jolly-Seber
	B	420	0.822 (0.034)	3		multi-strata models
	B	420	0.894 (0.029)	5		radio telemetry
Swainson's Hawk <i>Buteo swainsoni</i>	B	958.5	0.843 (0.019)	4	Schmutz <i>et al.</i> (2006)	
Galapagos Hawk <i>B. galapagoensis</i>	B	1099	0.94	3	Rivera Parra <i>et al.</i> (2012)	before goat eradication
	B	1099	0.84			after goat eradication

Ferruginous Hawk <i>B. regalis</i>	B	1468.5	0.708 (0.024)	4	Schmutz <i>et al.</i> (2008)	
Eurasian Buzzard <i>B. buteo</i>	B	875	0.88 (0.03)	5	Kenward <i>et al.</i> (2000)	
Northern Crested Caracara <i>Caracara cheriway</i>	M	1220	0.876 (0.003)	5	Morrison (2003)	
	F	1117	0.906 (0.002)			
Lesser Kestrel <i>Falco naumanni</i>	B	152.5	0.706*	3	Hiraldo <i>et al.</i> (1996)	multiple annual estimates
	B	152.5	0.67 (0.06)	3	Prugnolle <i>et al.</i> (2003)	
	B	152.5	0.72 (0.015)	3	Serrano <i>et al.</i> (2005)	large colonies
	B	152.5	0.653 (0.019)			medium colonies
	B	152.5	0.647 (0.019)			small colonies
Mauritius Kestrel <i>F. punctatus</i>	B	152.5	0.718 (0.013)	3	Mihoub <i>et al.</i> (2010)	
	B	119.5	0.782	3	Nicoll <i>et al.</i> (2003)	
	B	119.5	0.8 (0.04)	3	Nicoll <i>et al.</i> (2004)	hacked birds
	B	119.5	0.8 (0.04)			fostered birds
American Kestrel <i>F. sparverius</i>	B	119.5	0.75 (0.03)			wild-bred birds
	M	120	0.75 (0.05)	3	Hinnebusch <i>et al.</i> (2010)	
	F	111	0.74 (0.04)			

Sooty Falcon <i>F. concolor</i>	B	235	0.656 (0.069)	3	McGrady <i>et al.</i> (2015)	
Aplomado Falcon <i>F. femoralis</i>	B	341.5	0.91	3	Brown <i>et al.</i> (2006)	wild-bred breeder
	B	341.5	0.91			hacked breeder
	B	341.5	0.872			wild-bred non-breeder
	B	341.5	0.303			hacked non-breeder
Merlin <i>F. columbarius</i>	B	117	0.62 (0.11)	3	Lieske <i>et al.</i> (2000)	
Prairie Falcon <i>F. mexicanus</i>	F	908	0.87	3	Steenhof <i>et al.</i> (2006)	without transmitters
	F	908	0.49			with transmitters
Peregrine Falcon <i>F. peregrinus</i>	F	959	0.788 (0.031)	3	Gould & Fuller (1995)	
	B	598	0.725 (0.023)	3	Johnstone (1997)	
	M	598	0.765 (0.038)	3		
	F	959	0.701 (0.032)	3		
	B	814.5	0.859 (0.025)	4	Kauffman <i>et al.</i> (2003)	
	B	814.5	0.800 (0.054)	4	Craig <i>et al.</i> (2004)	
	M	598	0.73 (0.02)	3	Franke <i>et al.</i> (2011)	
	F	959	0.73 (0.02)			
	B	824.5	0.81	3	Faccio <i>et al.</i> (2013)	
	B	650	0.852	6	Altwegg <i>et al.</i> (2014)	
B	697.5	0.810 (0.034)	4	Smith <i>et al.</i> (2015)		

B. Owls

Common Barn Owl <i>Tyto alba</i>	B	403	0.720 (0.044)	4	Altwegg <i>et al.</i> (2003)	
	B	403	0.570 (0.023)	4	Altwegg <i>et al.</i> (2006)	
Snowy Owl <i>Bubo scandiacus</i>	F	2279	0.923 (0.057)	5	Therrien <i>et al.</i> (2012)	best case
	F	2279	0.852 (0.07)			worst case
Eagle owl <i>B. bubo</i>	B	2686	0.606	6	Schaub <i>et al.</i> (2010)	
Tawny Owl <i>Strix aluco</i>	B	475	0.755 (0.026)*	4	Francis & Saurola (2002)	capture-mark-recapture models
	B	475	0.760 (0.020)*			hierarchical model
	B	475	0.683 (0.035)*			capture-mark-recapture models, poor vole years
	B	475	0.727 (0.039)			hierarchical model, poor vole years
	B	475	0.736 (0.035)*			capture-mark-recapture models, medium vole years
	B	475	0.780 (0.035)			hierarchical model, medium vole years
	B	475	0.846 (0.025)*			capture-mark-recapture models, good vole years
	B	475	0.780 (0.036)			hierarchical model, good vole years

Spotted Owl <i>S. occidentalis</i>	B	475	0.739 (0.059)*	3	Karell <i>et al.</i> (2009)	experienced breeders **
	B	475	0.570 (0.070)*			first-time breeders**
	M	524	0.79 (0.03)	3	Millon <i>et al.</i> (2010)	
	F	426	0.86 (0.03)*			
	B	475	0.710 (0.029)	3	Pavón-Jordán <i>et al.</i> (2013)	two yrs old and >3 yrs old
	F	646	0.814 (0.050)	3	Seamans <i>et al.</i> (1999)	
	F	646	0.832 (0.029)			
	B	0.86	0.86	3	Bond <i>et al.</i> (2002)	
	B	606	0.82 (0.03)	3	Zimmerman <i>et al.</i> (2007)	
	M	566	0.843 (0.020)	3	Blakesley <i>et al.</i> (2010)	
	F	646	0.811 (0.021)			
	M	566	0.840 (0.017)			
	F	646	0.848 (0.016)			
	M	566	0.890 (0.016)			
	F	646	0.885 (0.016)			
	M	566	0.848 (0.015)			
	F	646	0.848 (0.015)			
	M	566	0.819 (0.013)	3	Forsman <i>et al.</i> (2011)	
	F	646	0.819 (0.013)			
	M	566	0.863 (0.008)			
F	646	0.859 (0.009)				
M	566	0.851 (0.007)				
F	646	0.853 (0.007)				
M	566	0.864 (0.010)				

	F	646	0.865 (0.010)			
	M	566	0.857 (0.013)			
	F	646	0.854 (0.014)			
	M	566	0.847 (0.080)			
	F	646	0.848 (0.080)			
	M	566	0.846 (0.009)			
	F	646	0.844 (0.009)			
	M	566	0.852 (0.014)			
	F	646	0.828 (0.016)			
	M	566	0.844 (0.018)			
	F	646	0.841 (0.019)			
	M	566	0.853 (0.010)			
	F	646	0.851 (0.010)			
	M	566	0.857 (0.008)			
	F	646	0.856 (0.008)			
	M	566	0.847 (0.040)*	3	Ganey <i>et al.</i> (2014)	annual estimates 2004-2009
	F	646	0.859 (0.036)*			annual estimates 2004-2009
	B	606	0.828	6	Tempel <i>et al.</i> (2014)	
Ural Owl <i>S. uralensis</i>	B	785	0.80 (0.016)	3	Pavón-Jordán <i>et al.</i> (2013)	
Little Owl <i>Athene noctua</i>	M	164	0.651 (0.043)	3	Schaub <i>et al.</i> (2006)	
	F	164	0.610 (0.042)			
	M	164	0.673 (0.033)			
	F	164	0.674 (0.026)			
	F	164	0.687 (0.068)			
	M	164	0.740 (0.057)			

Burrowing Owl <i>A. cunicularia</i>	F	164	0.659 (0.051)			
	B	164	0.753 (0.019)	3	Le Gouar <i>et al.</i> (2011)	
	B	164	0.66	5	Thorup <i>et al.</i> (2013)	
	M	146	0.81 (0.04)	3	Millsap (2002)	highly developed area
	F	156	0.69 (0.04)			highly developed area
	M	146	0.62 (0.05)			moderately developed area
	F	156	0.69 (0.04)			moderately developed area
	B	151	0.545	4	Barclay <i>et al.</i> (2011)	
	B	151	0.71			increasing population
	B	151	0.465			decreasing population
	M	146	0.44 (0.05)	3	Wellicome <i>et al.</i> (2014)	
	F	156	0.21 (0.03)			
Boreal Owl <i>Aegolius funereus</i>	B	142	0.46	5	Hayward <i>et al.</i> (1993)	

*geometric mean of different estimates (see text)

**during periods of low, increasing and decreasing population

Figure 1

