Using recruitment age, territorial fidelity and dispersal as decisive tools in the conservation and management of peregrine falcon (*Falco peregrinus*) populations: the case of a healthy population in Northern Spain

Iñigo Zuberoigoitia · Jose Antonio Martínez · Ainara Azkona · Jose Enrique Martínez · Iñaki Castillo · Jabi Zabala

Received: 14 December 2007 / Revised: 16 April 2008 / Accepted: 13 May 2008 / Published online: 4 June 2008 © Dr. Ornithologen-Gesellschaft e.V. 2008

Abstract Methods of evaluating population trends have recently received particular attention because of perceived declines in several species during the twentieth century. We have studied demographic traits of the peregrine falcon (*Falco peregrinus*) population in Bizkaia (Northern Spain) for 11 years. This species suffered a severe decline in the 1950s and 1960s and started to recover in the 1980s and 1990s, although the recovery trends differed between areas. In our study area the peregrine falcon density is one of the highest found in Spain. The frequency of juvenile breeders was 2.0%, the mean age at first breeding being 3.7 calendar years for males and 4.0 cy for females. The territorial fidelity was at least 3.4 years for males and 3.7 years for females. Females dispersed on average 80.5 km and males 51.8 km during their pre-breeding movements, whilst distance between birthplace and breeding territories was on average 108.5 km for females and 64.5 km for males. We studied the relationships between adult turnover, recruitment age, territorial fidelity and dispersal in a healthy population in order to establish population dynamics. A combination of these parameters, not just age at first breeding, could be used as a potential early warning signal indicating future changes, prompting their consequences to be evaluated. This approach could lead to the reclassification of the large-scale health of a population. Its utilization would allow resources to be directed into helping “ailing” subpopulations, detecting causes of decline, and developing adequate recovery strategies.

Keywords Age at first breeding · Dispersal · Territorial fidelity · Turnover rate · Early warning signals

Introduction

In long-lived species, adult survival is the factor most closely correlated with future population trends (Stearns 1976). Environmental factors affecting adult survival are likely to have a higher impact on population trends than factors affecting fecundity or dispersal (Benton and Grant 1996). However, adult survival is usually difficult to measure, since it requires a considerable investment of effort, time and money. In fact, the turnover rate is underestimated in most studies, because researchers are unable to identify replacement adults (Pandolfi et al. 2004). Thus, occupancy is used as an alternative measure (see, e.g., Balbontin et al. 2003; Sergio and Newton 2003; Martínez et al. 2008).

The age of breeding individuals is also an important demographic factor, because it is correlated with reproductive performance (Henny et al. 1970; Newton 1979, 1989; Penteriani et al. 2003; Pandolfi et al. 2004). The age
of first breeding may be used as a signal to detect population trends in long-lived species (Balbontín et al. 2003). Breeding success of immature individuals and adult mortality rate are correlated in species such as the peregrine falcon (Falco peregrinus) (Ratcliffe 1993). Birds with immature plumage are capable of breeding, but do not normally do so because any gaps in the territorial system are usually filled by older birds. However, when the death rate increases, more territories become vacant, enabling younger birds to breed (Newton 1979).

Density, adult turnover and recruitment age could also be decisive factors regulating individual dispersal. Post-fledging movement before and during the initial stages of dispersal is an inherent component of subsequent ecological processes and, logically, influences future demographic or distributional patterns (Matchunts et al. 1996). Some research suggests that individuals that disperse earlier are in better physical condition than late dispersers (Belthoff and Dufy 1998; Willey and van Riper 2000), although density-dependent social interactions can affect dispersing raptors (Dziulak et al. 2005).

The long-term monitoring of animal abundance and distribution has been used to determine the status and trends of populations. However, census techniques detect changes in population trends once they have already occurred, and therefore lack predictive capability (Balbontín et al. 2003; Ferrer et al. 2003; Pandolfi et al. 2004).

The peregrine falcon is a wide-ranging, long-lived raptor with a maximum lifespan of 21 years in the wild (Ratcliffe 1993; Zuberoagotia et al. 2002). Some peregrine populations, particularly those from the far north, migrate over long distances (i.e., Ganusevich et al. 2004), whilst others are sedentary (Cade et al. 1988; Ratcliffe 1993). The species suffered a severe decline in the 1950s and 1960s due to the toxic effects of persistent residues of organochlorine pesticides ingested via prey species (Ratcliffe 1993). Following phased withdrawals or bans on the use of most organochlorines, there have been variable recoveries of affected populations (Ratcliffe 1997).

The last census of Spanish peregrine falcons estimated the population at 2,384–2,690 breeding pairs (Gainzarain et al. 2002). Gainzarain et al. (2003) considered that although the population seemed to be increasing, more effort was needed to evaluate the trends in some unknown areas and to know more about the process associated with decline in others. In our study area, the peregrine density is one of the highest found in Spain (Zuberoagotia et al. 2002) and has been stable over the last decade. In this context, our main aim was to investigate the relationships between adult turnover, recruitment age, territorial fidelity and dispersal in a healthy population in order to evaluate such data for use in conservation management.

Study area

The study area (2,384 km²) was the province of Biscay (North of Spain). Man-made forests, pastures, small villages and densely populated cities make up the bulk of the province. The terrain is rugged, and elevation ranges from sea level to 1,500 m in the Basque Mountains. The weather is temperate, with annual rainfall of 1,000–1,300 mm and mean annual temperatures of 11–12 °C (Loidi 1987).

Methods

Data collection

The peregrine falcon population in Biscay was censused between 1997 and 2007 (Zuberoagotia 1997; Zuberoagotia et al. 2002). Of 52 breeding territories found, we systematically monitored 37. From 20 February until 20 April we spent 22 days every year searching for adults in breeding territories. Six researchers, divided into two teams using three 20 x 60 Swarovsky AT6 80 and binoculars, spent approximately 1,320 h per year monitoring adult peregrines.

Peregrines were identified as second calendar year (cy) when they showed total or partial juvenile plumage, third cy when they retained some juvenile feathers in an adult plumage, and third or more cy when they showed an entirely adult plumage (Mearns and Newton 1984b; Forsman 1999; Zuberoagotia et al. 2002). It is not possible to identify more age classes in the field.

Territorial fidelity was measured as the number of observed years in which a falcon occupied the same territory. Some peregrines, logically, were already occupying the breeding site when we started the study, while some of these and others continued to occupy the same site after the end of the study period (11 years). Therefore, territorial fidelity represents the minimum occupation.

Recruitment age, territorial fidelity and dispersal were also measured using ringing control data. First, we considered all of the control data for dead or injured falcons that were recovered thanks to the official ringing scheme (Aranzadi-San Sebastian Ringing Office); second, we compiled every observation of ringed falcons in the wild. The reading of alphanumeric rings in the study area was conducted only by our research team, whilst those done out of the study area were supplied by other ornithologists.

Statistical analysis

The data set was analyzed by nonparametric tests: ANOVA, Kruskal–Wallis and Mann–Whitney tests. Transformations were not considered in order to develop
parametric tests (Krebs 1989). Statistical significance was set at $p < 0.05$. All tests were computed using the SPSS 15.0 software package.

Results

During the study period, we ringed 426 chicks and 16 adults (eight males and eight females) with official rings and colored rings with an alphanumeric code for long-distance observation. We individually identified 35 territorial peregrines from their alphanumeric rings.

Overall, 11 (one male and ten female) young peregrines were detected in nesting territories in a total of 272 breeding attempts during 11 years (Table 1). This means that 2.0% of the established peregrines were second cy. The proportion of nests of the mixed (young and adult) pairs that produced young was 36.4%, significantly less than the corresponding value of 68.7% for the adult pairs ($X^2 = 4.76, p = 0.029$).

Considering individual monitoring, 74 different territorial peregrines were aged 2cy, 3cy or >3cy in breeding territories over the 11 years, 14 of which were ringed at the breeding site and monitored over successive years. The frequency of second cy breeders was 3.3% for males and 22.7% for females, whilst those of third cy were 6.6% for males and 6.8% for females, and those of third or more cy were 90% for males and 70% for females (Table 1). Thirteen peregrines ringed in the nest were later recorded as first-time breeders in the study area at 3.7 cy (SD = 0.7) for males and 4.0 cy (SD = 1.4) for females. Nine peregrines ringed in the nest in the study area were recorded later as breeders out of the study area at 3.5 cy (SD = 0.7) for males and 3.0 cy (SD = 1.3) for females. There were significant differences between groups (ANOVA, Kruskal–Wallis test, $H = 23.085, p = 0.000$). The ages of both sexes obtained by observing plumages were significantly less than when using ringed birds. This was because we can only ascertain age up to third cy in the wild using plumage characteristics. The age of first-time occupancy was less in females than in males ($U$ Mann–Whitney test, $U = 848.5, p = 0.012$).

The territorial fidelity of a peregrine falcon in the study area was at least 3.4 years for males (SD = 2.5, range = 1–10, $n = 28$) and 3.7 years for females (SD = 2.6, range = 1–10, $n = 32$). There were no differences between sexes (Mann–Whitney test, $U = 492.5, p = 0.701$).

Once flying, young peregrines started to move quickly, finding females 5.5, 9.3 and even 47.5 km away from the nest site during the first month, whilst two males were found at 6.8 and 323 km in the first month. Most of them came back to the nesting site and asked for quarry from their parents. One female was repeatedly seen with her parents until the last week of November.

Females moved on average 80.1 km during their pre-breeding dispersal (Table 2). There were no significant differences between the dispersal distances in summer, winter and after one year (ANOVA, Kruskal–Wallis test, $H = 5.288, p = 0.071$). One female was seen at the birth site one year later, during her second calendar year, sharing perches with her parents; she had not been seen before and nor was she seen later. Males moved on average 51.8 km during the pre-breeding season. There were no significant differences between the dispersal distances in summer, winter and after one year (ANOVA, Kruskal–Wallis test, $H = 0.852, p = 0.653$). There were no statistical differences between the dispersal distances of the sexes (Mann–Whitney test, $U = 92.5, p = 0.80$).

Females were located breeding on average 108.5 km away from the birthplace and males were located 64.5 km from the birthplace. There were no significant differences

<p>| Table 1 | Age at first breeding for peregrine falcons, considering (a) falcons monitored in their territories (60 individually identified from individual markings and 14 trapped and ringed), (b) 13 falcons that were ringed as chicks in the study area and were first-time breeders in a territory within the study area, (c) 9 falcons that were ringed as chicks in the study area and were first-time breeders in a territory outside the study area |</p>
<table>
<thead>
<tr>
<th>Age (Calendar year)</th>
<th>Falcons monitored in territories</th>
<th>Ringed falcons breeding within the study area</th>
<th>Ringed falcons breeding outside the study area</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>2cy</td>
<td>1</td>
<td>10</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>3cy</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>&gt;3cy</td>
<td>27</td>
<td>31</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>4cy</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>5cy</td>
<td>30</td>
<td>44</td>
<td>9</td>
<td>4</td>
</tr>
</tbody>
</table>
between post-fledging dispersal and natal dispersal in females (Mann-Whitney test, $U = 52.5, p = 0.18$), or in males (Mann-Whitney test, $U = 75, p = 0.913$), although females tended to move further than males for breeding (Mann-Whitney test, $U = 28, p = 0.033$, Fig. 1).

**Discussion**

Unlike in other parts of the peregrine breeding range, the breeding population in the study area remained stable or increased slightly during the period 1997–2007. After the recovery of the Spanish population in the 1980s, some areas in the middle and the south of the country started to detect a decline (Gainzaran et al. 2002; Zuberogoitia et al. 2002). Some monitoring teams detected a high number of second cy peregrines trying to nest, implying a high turnover rate (Zuberogoitia 2005), possibly due to high organochlorine levels (Merino et al. 2005) and predation from increasing numbers of eagle owls (*Bubo bubo*) (Martínez and Zuberogoitia 2003). Afterwards, territories started to disappear on a large scale. Meanwhile, the population trend in North Spain continued upwards, and the territorial density was the highest detected in recent history (Zuberogoitia et al. 2002).

Nowadays, the trends and population dynamics of a species in an area are not related to simply the number of breeding pairs and their spatial distribution (Ferrer et al. 2003). In fact, even with a relatively stable number of peregrine breeding pairs, the overall trends could be negative due to a high turnover rate (Pandolfi et al. 2004). The number of territories remains stable, but the total number of birds in the population (breeders and floaters) decreases. Balbontin et al. (2003) proposed that regular monitoring of the age structure of territorial pairs of long-lived bird species may have predictive power when using demographic traits and, consequently, could be used as an early warning signal for changes in population viability. An increase in birds without adult plumage within the breeding portions of populations of species with deferred maturity could be a consequence of temporal reductions in adult survival rates that could lead to a future decrease in population size. Hence, it should be possible to anticipate an impeding population decline before breeding numbers start to decrease.

According to Tordoff and Redig (2003), the low proportion of immature breeding falcons found in our study area could be a decisive factor when evaluating the population health. In fact, the breeding success of mixed pairs was significantly lower than the observed rate in adult pairs, as also found for other populations and other species (Meurn and Newton 1984b; Balbontin et al. 2003; Ferrer et al. 2003; Pandolfi et al. 2004; Martínez et al. 2008). The probability of detecting non-adult falcons in a territory is high due to the easy identification of juvenile plumage. Thus, upon employing this system, we obtained an immature proportion of 2.0%, which can be compared with other published rates (0–13% annually in 1974–82 in

![Fig. 1 Dispersal distances versus time elapsed for peregrine falcons.](image) Distance from the birth site to breeding sites (smaller circles), observed via the colored rings with alphanumeric codes; post-fledging sites (large circles), observed via the colored rings and dead ringed animals that were recovered.

© Springer

It may be better to establish a new parameter for evaluating population trends that accounts for the average age at first breeding in a controlled population. The recruitment age in the studied population was 3.7 years for males and 4 years for females, considering the ringing data, which could be slightly less when using plumage identification because we can only ascertain age up to third cy in the wild. According to Court (1986), this rate implies that peregrine falcons spend more than three years in the floater population waiting for a chance to occupy a territory. In this context the occasional presence of immature falcons could be related not only to the two possible causes suggested by Balbotin et al. (2003), an increase in adult mortality rate or an increase in the availability of resources such as nest sites or food supply, but it could also be related to individual fitness and the ability to obtain a resource (territory) in a highly competitive environment (Tordoff and Redig 2003).

Moreover, our results show a relatively long lifespan for the territorial peregrines. We identified several peregrines which we had identified in 1997 and were still occupying the same territories in 2007. The minimum lifespan, expressed as the number of years during which one peregrine occupies the same territory during the 11-year period, seems to be high enough to keep the breeding population stable, especially if we consider that both sexes have the same lifespan. Turnover rate, then, was conditioned by the relatively high survival rate (see Mearns and Newton 1984a; Tordoff and Redig 2003; Kleinstäuber 2006), although the normal 21% rate increased to 30% due to the impact of the Prestige oil spill on the population (Zuberogoitia et al. 2006). Had this catastrophe not occurred, we might have seen higher rates of adult survival and further delays in mean recruitment age.

Considering that in our study area there were 32 breeding territories, the estimated number of peregrines involved in the population turnover (both territory owners and birds disappearing from the breeding population) during the 11-year study period would be 167 males and 153 females, including those that were occupying territories at the end of the period. At the same time, we ringed 426 chicks from 21% (1998) to 71% (2007) of the nests. Obviously, the number of fledglings, the net immigration from neighboring areas and the survival rate was higher than the adult turnover; were it not, a population decline would have been detected. These data would influence the length of time that a peregrine waits for a chance to breed (Newton 1979; Tordoff and Redig 2003). Three to four years is a long period for a species which can breed when it is one year old. During this time, some peregrines dispersed over long distances to look for a territory in a low-density area. This would explain why 57.1% of the long-distance females settled in a territory and bred during their first year, and it would explain why the dispersal movements of other low density populations were much less (see, e.g., Mearns and Newton 1984a, 1984b; Cade et al. 1988; Ratcliffe 1993; Zuberogoitia et al. 2002; Dziak et al. 2005; Kleinstäuber 2006).

Peregrines started to move at an early age (Fyne 1988; Powell et al. 2002), with ringing records showing long movements during the month after the first flight. Nevertheless, some young stayed in the parental territories for several months, and we detected occasional visits of some of the young to the parental territory or neighborhood one year later. We suggest that the decision to disperse for long or short distances could be an individual behavior that is not associated with sex. On the one hand, some peregrines could spend their first years floating around the birthplace, waiting for a vacancy. In our study area, where a high density population exists, this could be an expensive strategy, because the bird would lose several years waiting for a chance to breed, and the aggressions associated with territorial defence result in potentially harmful fights between adults (Zuberogoitia et al. 2002). However, the knowledge of the territory gained in this way could be advantageous in later life (Tordoff and Redig 2003). On the other hand, some peregrines quickly moved long distances, establishing themselves in low-density areas. Surprisingly, according to Ratcliffe (1993), the distances recorded for the dispersing young were no longer than those for breeding birds. In conclusion, the population surpluses of one area, such as ours, could help other areas recover—even areas more than 300 km away.

Our results support previous findings, showing the importance of long-term studies of demographic traits in long-lived territorial species characterized by deferred maturity. However, we consider more factors in order to fully understand the dynamic mechanism in a population. We not only considered the age at first breeding, the adult turnover and the productivity, but we also identified the occupancy (the number of years that one bird maintains a territory) and the dispersal. In this way, each change in the population could be detected quickly and its consequences evaluated, allowing the anticipation of future trends.

In this research we emphasize the importance of monitoring healthy populations, not only those suffering severe declines, in order to prevent problems from developing. In fact, our population is working as a source where births exceed deaths, and is sending surpluses to other areas in which death rates are unsustainably high.
The most recently published list of endangered Spanish bird species de-listed the peregrine falcon, considering it to be no longer threatened (Madroño et al. 2005). However, it must be noted that the health of the national population was evaluated using numbers of territories and their trends compared with previous censuses, which could not have been accurate since other factors such as those explained above were not taken into account (Gainzarain et al. 2003). Had the “early warning signals” been considered, this latest decision might have been different, at least for Central, Southern and Eastern Spain.

We, therefore, recommend monitoring subpopulation symptoms in order to predict declines in advance. Resources should then be directed into helping “ailing” subpopulations, detecting causes of decline and developing adequate recovery strategies.

Zusammenfassung

Rekrutierung, Revierfreue und Dispersion als ausschlaggebende Schlüssel faktoren für Schutz und Management von Wanderfalkenpopulationen (Falco peregrinus) am Fallbeispiel einer gesunden Population in Nordspanien


Acknowledgments We thank L. Astorkia, F. Ruiz Monco, J. Zaherogotia, S. Hidalgo, C. González de Buírrago, J. Elorriaga, J. Isasi, J. Fernández, I. Patracs and J. Illarramendi for their field assistance. Juli Sagardia, Oscar Prada, Javier López, Jesús Garcia, José Luis Rodríguez, Alejandro Ortuño, Arturo Rodríguez, Gorka Belamendi and Ekos provided us with data for ringed peregrine falcons breeding in sites outside our study area. This research was partially funded by the Biodiversity Department of the Basque Government and the Agricultural Department of Diputación Foral de Bizkaia, which also issued the licences to work with this species. We thank the Ringing Office of San Sebastian, who helped with the material for ringing. We also thank Sally Leigh for linguistic revision and Gert Kleinstäuber and two anonymous reviewers for their helpful and constructive comments on an earlier version of the manuscript.

References


Court GS (1986) Some aspects of the reproduction biology of tundra Peregrine Falcons. MSc thesis, University of Alberta, Edmonton, Canada


© Springer


