

Understanding the coexistence of competing raptors by Markov chain analysis enhances conservation of vulnerable species

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Abstract

Understanding ecological interactions among protected species is crucial for correct management to avoid conflicting outcomes of conservation planning. The occurrence of a superior competitor may drive the exclusion of a subordinate contestant, as in Sicily where the largest European population of the lanner falcon is declining because of potentially competing with the peregrine falcon. We measured the coexistence of these two ecologically equivalent species through null models and randomization algorithms on body sizes and ecological niche traits. Lanners and peregrines are morphologically very similar (Hutchinson ratios <1.3) and show 99% diet overlap, and both of these results predict competitive exclusion. In contrast, their use of diverse cliff substrates for breeding in different times of the season would predict coexistence. To compare these two mutually excluding hypotheses, we examined the pattern of inter-specific transitions in 88 sites that were studied for 14 years (2000–2013) using a Markov chain (MC) occupancy state model, and checked the sensitivity and elasticity of the community structure to changes in transition probabilities. During the study period, 1144 territorial transitions occurred in peregrine and lanner territories, and the MCs were predicted to converge to a stable equilibrium in 2065. Markovian analysis suggested that temporal and spatial segregation of habitat during reproduction might prevail over anatomical specialization for hunting and diet, allowing species coexistence, despite the prediction that peregrines will outnumber the lanners in future projections. Our approach combining niche-overlap analysis and species occupancy modelling led to practical information about conservation options available for the threatened lanner. Lanners are very sensitive to site abandonment, and measures increasing adult persistence in occupied territories could be more rewarding than those encouraging juvenile dispersal and colonization of new sites.

Introduction

Niche theory predicts that coexisting species should differ in ecological, morphological or behavioural characteristics in a way that minimizes competition (Hutchinson, 1959). The ability to compete is usually different among species, and ecological interactions occurring for limited resources are asymmetrical, with the dominant species reducing the fitness of subordinate ones by constraining their utilization of preferred resources (e.g. Campobello, Hare & Sarà, 2015). The latter is typical of interference competition (Amarasekare, 2002), which will have different long-term effects depending on its strength, ranging from stable coexistence to competitive exclusion (Tokeshi, 1998).

Many drivers, such as body size and social system (e.g. García & Arroyo, 2002), human disturbance and the harshness of environmental gradients (e.g. Moreno-Rueda *et al.*, 2009; Miller *et al.*, 2012) and more recently, invasive species (e.g. Santulli *et al.*, 2014), have been claimed to alter resource availability and in turn the outcome of competitive interactions. In general, the higher the niche-overlap value between two species, the less likely it is that there will be long-term population coexistence (Krüger, 2002a,b). In addition, phylogenetic niche conservatism has been suggested to enhance the likelihood of inter-specific competition (Losos, 2008).

The importance of competition has been emphasized at high trophic levels (Hakkarainen *et al.*, 2004). Since most raptors are long-lived territorial species and show great fidelity to their

breeding areas (Newton, 1979), the habitat around their nest and features of the nest site itself are closely associated with breeding success (Sarà, Campobello & Zanca, 2012; Amato *et al.*, 2014) and hence influence fitness (Bosakowski, Smith & Speiser, 1992). As a consequence, when habitat conditions limit the breeding space of cavity-nesting *Falco* species, the need for favourable nesting habitats may drive intense intra-specific or inter-specific competition (e.g. Brambilla *et al.*, 2010).

Conditions regulating species coexistence are not only relevant *per se*, but are more stimulating when the species in question are of conservation concern. This is particularly important when the occurrence of a superior competitor may lead to competitive exclusion or may limit the density of a subordinate and threatened competitor (López-López *et al.*, 2004; Oro *et al.*, 2009). Current implementation of environmental policies and laws generally ignore inter-specific effects (Soulé *et al.*, 2003), which may in turn generate unexpected and conflicting consequences on the practical effects of conservation management actions (e.g. Thirgood *et al.*, 2000; Roemer & Wayne, 2003).

Checking territorial occupancy is a reliable method for the assessment of spatiotemporal variations in territory quality of raptors (Sergio & Newton, 2003). Since most processes affecting species interactions are stochastic (e.g. human disturbance) and the interpretation of results based on static approaches may be misleading (Miller *et al.*, 2012), a valid dynamic approach to the investigation of community interactions is the estimation of site transition probabilities that determine species occupancy by using Markov chain (MC) models (Hill, Witman & Caswell, 2002, 2004). MCs were first used in animal ecology to model successional changes (Waggoner & Stephens, 1970; Tanner, Hughes & Connell, 1994), and they are now attracting attention for application in the study of population dynamics of vulnerable species (López-López *et al.*, 2009; Martin *et al.*, 2009a; Jiménez-Franco, Martínez & Calvo, 2011).

In this paper, we study two falcon species – the peregrine *Falco peregrinus brookei* and the lanner *F. biarmicus feldeggii* – that live sympatrically in the Mediterranean island of Sicily (Italy). All members in the Falconidae form a monophyletic group (Fuchs, Johnson & Mindell, 2015) and although peregrine and lanner are not sister species, they have high morphological similarity in their anatomical specializations for hunting. Both species show territorial behaviour, usually nest on cliffs and need open habitats for hunting, and so many populations are sympatric in steppe-like habitats (Ferguson-Lee & Christie, 2001). Birds caught in aerial chases form the total of peregrine prey and most of the lanner prey biomass. The lanner falcon can also feed on a variable frequency of reptiles, small mammals and insects, although these confer a low biomass contribution (Ferguson-Lee & Christie, 2001; Andreotti & Leonardi, 2007). For these reasons, a high degree of phylogenetic niche conservatism (Losos, 2008) might be expected and this in turn would drive the potential interference between coexisting populations of the two falcons.

Importantly both species are protected, and included in Annex I of the 2009/147/EC Bird Directive. They are listed in the 'least concern' category by the IUCN (2011) global assessment. Nonetheless, while the peregrine is still a least-concern

species in the European Union, the lanner has an unfavourable conservation status, due to its small and declining populations and dispersal range, and has been listed as a vulnerable species in the Italian Red list (Birdlife International, 2004; Peronace *et al.*, 2012).

Sicily hosts the largest European population of *F. b. feldeggii* (Andreotti & Leonardi, 2007). Recently, spatial analysis of lanner habitat preferences in Sicily suggested that the alteration of traditional agro-ecosystems might enhance interference competition with the peregrine and limit its occupancy (Sarà, 2014), thus reinforcing hypotheses of competitive interactions between the two species (Sarà, 2008).

As the coexistence of ecologically equivalent species is rare in islands due to their smaller size and larger isolation with respect to continents (Gotelli & Mc Cabe, 2002), a careful quantitative investigation of the ecological relationships between these two potentially competing species is necessary to avoid the failure of conservation planning (Sergio & Hiraldo, 2008) and to design specific management actions aimed at mitigating the lanner population decline in its Mediterranean core range.

In particular, the aims of this paper were to (1) investigate the potential competitive effects of the peregrine on lanner occupancy of breeding territories by performing a MC occupancy state model on the patterns of inter-specific site transitions; (2) examine through perturbation analysis the sensitivity and elasticity of the community structure to changes in transition probabilities and (3) simulate the effects of potential management strategies aimed at increasing the number of territories occupied by the most vulnerable lanner and to assess their impact on long-term population dynamics.

Materials and methods

Study area

Sicily, the largest Mediterranean island, was selected as a study area representative of the lanner falcon range. It covers 25 832 km² and is the largest (8.6% of the national surface) and one of the most populated (197 inhabitants per km²) administrative regions of Italy. Almost 24.4% of the territory is mountainous, 61.4% is composed of highlands and 14.2% of the surface is lowland. Natural vegetation has been greatly reduced by human influence, and forests occupy only 8% of the territory, mostly in the northern region. There is considerable habitat heterogeneity in the hilly and flat inland areas, where arable land, fodder, vineyards and olive orchards alternate with woodlots of non-native species (*Pinus* spp. and *Eucalyptus* spp.), natural evergreen woodlands (*Quercus* spp.), Mediterranean xeric grasslands and shrub vegetation. The climate is Mediterranean, but annual precipitation is highly variable and increases with elevation.

Population monitoring

Accurate occupancy datasets of lanners and peregrines in Sicily were available from past surveys carried out for the third Atlas of Breeding Birds of Sicily (AA.VV., 2008), and from other specific surveys (Andreotti & Leonardi, 2007; Sarà, 2008).

From these datasets, we selected a large area of sympatry of the two falcons that covered 10 200 km². In this area, with the aid of collaborators that are well versed in the identification and ecology of falcons, we intensively searched and monitored falcon territories, gathering information on 168 sites occupied by falcons. As not all sites were checked every year, we restricted our analysis to 88 territories from which we were able to gather complete occupancy data during the 2000–2013 breeding seasons. For the purposes of this study, the occupancy of both falcons was expressed in terms of territorial pairs, irrespective of breeding output. We considered as a ‘territory’ a site, often an entire cliff, plus a portion of the surrounding land defended exclusively by each species. Therefore, by definition, both species could not coexist in the same territory. All selected territories were visited at least three times during each breeding season, from late January to mid June, to assess occupancy. During the study period, 75 territories were occupied in at least 1 year, by territorial pairs of falcons, while 13 remained vacant. These latter represented a sample of sites where records (killings and/or observations of transient adults and juveniles) were reported in the past (M. Sarà, R. Mascara and B. Massa, unpubl. data). Special care (i.e. extra visits) was taken to ensure that territorial pairs were effectively not present in vacant territories or to detect where they moved in case of site desertion. Observations were made using 10 × 42 binoculars and 20 × 60 telescopes (Leica, Solms, Germany) on clear days and from 200 to 500 m away from the nesting cliffs to avoid disturbance.

Assessing the degree of competition between lanner and peregrine

We quantified the overlap of body sizes and some traits (see Supporting Information Appendix S1 and Tables S1 and S2) of the ecological niche between lanner and peregrine by using null models and randomization algorithms (Gotelli & Graves, 1996), provided in Ecosim 7.0 Software (Gotelli & Entsminger, 2001), in order to better understand the ecological equivalence of both falcons (see Supporting Information Appendix S1, for rationale and computational details). Results (see Supporting Information Tables S1 and S2) obtained from our quantitative approach allowed us to set two mutually exclusive hypotheses and related predictions as follows: (1) if equally high anatomical specialization for hunting and diet exists, then phylogenetic niche conservatism would predict the competitive exclusion of one species from Sicily; (2) if spatial and temporal segregation of the breeding sites exists, then niche partitioning would predict the possible coexistence of the two species in the island.

Then, using the transition probabilities recorded at 88 falcon sites monitored over a period of 14 years, we tested the two predictions by means of MC analysis (MCA).

Markov chain analysis

We calculated the frequency with which territories used by each species in a given year were re-occupied by the same

species in the following year, usurped by the other, or abandoned, as well as the frequency with which empty territories were colonized by either lanners or peregrines, or remained unoccupied. These frequencies were used to calculate the transition probabilities and to build 13 transition matrices of a first-order Markov model for the study period (2000–2013). We started with the number of present territories of each species and those vacant in 2000 as the stage vector, and considered time steps of 1 year. According to our definition of territory and to previous MCA that estimated community interactions (e.g. Tanner *et al.*, 1994; Hill *et al.*, 2004), we assumed that all territories could be potentially occupied by both species and vacant territories could be colonized in the future. This prerequisite assumption of the study seems reasonable because according to our field observations and those of Di Vittorio *et al.* (2015), cliff replacements between both species as well as colonization of vacant territories were recorded.

A finite-state MC reflects a stochastic process independent of time, in which the probability of moving from one state to the next (fate at time $t + 1$) is conditional on the present state (fate at time t). Therefore, we fitted log-linear models on the transition matrices to test whether our data were suitable to build a time-invariant MC (Caswell, 2001; Hill *et al.*, 2002).

Perturbation analysis

Sensitivity and elasticity, the two components of perturbation, allow the exploration of how changes in environmental conditions or management practices could affect the dynamics of the community in the long term (Caswell, 2007; Green, Bailey & Nichols, 2011). We explored the effects of changes in transition probabilities of the lanner, which has the worse conservation status, in order to identify management strategies that may improve the likelihood of population persistence. To that end, we explored the effects of increasing the probability of (1) persistence of lanner territories (coded as L-L, which reads lanner to lanner), thus reflecting decisions that decrease lanner adult mortality and/or discourage the abandonment of its occupied territories; (2) replacement from territories occupied by peregrines to those occupied by lanner (P-L); (3) transition from vacant territories to those occupied by lanners (E-L), thus modelling a potential scenario in which the mortality of juvenile lanners decreases, and/or lanner colonization of new territories is encouraged. Changes were modelled by iteratively increasing the probability of transition of the variable of interest to 1, 2.5 and 5% (Caswell, 2001; López-López *et al.*, 2009). One of the essential properties of MC is that they require column totals to sum to 1, and so it is not possible to modify only one variable while holding all others constant (Caswell, 2001). Hence, the two transition probabilities of compensatory variables in the same column were modified iteratively by decreasing their respective value by the same quantity as that of the transition of interest and keeping the third constant. For instance, a 1% increase in the E-L transition probability was compensated by a 1% decrease in the E-P transition probability while keeping the E-E transition probability constant. This allowed us to assess the relative effect of changes in transition probabilities

in the population dynamics of the two species given that Markov models converge to a stationary equilibrium in the long term (Caswell, 2001; Hill *et al.*, 2004).

Transition matrices and the MC were analysed using the package 'markovchain' for R (Spedicato, 2015). Equilibrium occupancy was calculated according to Martin *et al.* (2009b) as: $\psi^* = \text{colonization}/(\text{colonization} + \text{extinction})$. Statistical significance was set at $P < 0.05$.

Results

Degree of competition between lanners and peregrines

Preliminary assessment gave information on the potential interactions between the lanners and peregrines living in Sicily (see Supporting Information Tables S1 and S2). Morphologically, they are very similar, and in fact the corresponding Hutchinson ratios were lower than 1.3 for size and 2.0 for body weight. Null model analyses of size overlap were not significant values ($P > 0.05$) for each tested trait ($n = 6$, Supporting Information Table S1), and thus the tests rejected the Hutchinson hypothesis of minimum morphometric spacing necessary for coexistence. Accordingly, the Pianka's niche-overlap indices (PI) for diet (Supporting Information Table S2) indicated the use of identical resources ($PI_{\text{prey_biomass}} = 0.999$, and $PI_{\text{prey_frequency}} = 0.922$) and the results statistically deviated from those obtained by chance ($P = 0.00$ and 0.01 , respectively). Consequently, lanners and peregrines living in Sicily show a conspicuous similarity of anatomical traits for hunting (e.g. tarsus and bill sizes, Supporting Information Table S1) in connection with high diet overlap (Supporting Information Table S2). By contrast, nesting site characteristics ($PI_{\text{cliff_height}} = 0.242$, $P = 0.921$; $PI_{\text{cliff_substrate}} = 0.839$, $P = 0.446$) and Julian day of laying ($PI = 0.390$, $P = 0.867$) gave lower Pianka indices, which were not statistically different, thus indicating a spatial and temporal segregation of habitat during reproduction that would possibly predict species coexistence.

Markov chain analysis

A total of 1144 territorial transitions were recorded from 2000 to 2013 in the study area (Table 1), with the lanner showing a median \pm SD of 45.5 ± 3.8 occupied territories (min–max:

36–48) and the peregrine 21.0 ± 3.9 occupied territories (min–max: 16–28), while vacant territories were 23.5 ± 2.3 (min–max: 19–27). The transition matrix followed the assumptions needed to build a first-order time-invariant MC, as log-linear models showed no significant differences among the annual transition matrices over the study period ($\chi^2 = 58.12$, $df = 96$, $P = 0.99$).

According to the baseline scenario depicted in Table 1, if current conditions of time-invariance in transition probabilities persist, the projection of the sampled population in the 88 sites predicts convergence of the MC to a stable equilibrium in 2065, with 29 lanner pairs, 37 peregrine pairs and 22 empty sites (Fig. 1). Equilibrium occupancy was $\psi^* = 0.534$ for the lanner, whereas it was $\psi^* = 0.607$ for the peregrine. The final stable equilibrium would correspond to a 19% decrease in lanners, 32% increase in peregrines and an 8% decrease in empty sites in 2065 with respect to 2013 (36 lanners, 28 peregrines and 24 empty sites); however, there would be a remarkable 40% lanner decrease, 131% peregrine increase and 8% decrease in empty sites with respect to 2000. Nonetheless, the key point of the MCA is that a stable coexistence could occur in Sicily, with peregrines outnumbering lanners but without causing their extinction in the long term.

Perturbation analysis

Sensitivity showed diverse scenarios under the different management strategies modelled to increase the likelihood of lanner population persistence (Fig. 2). Measures aimed at increasing territory persistence by lanners (+LL in Fig. 2) led to the highest number of territories occupied by lanners, thus providing a more efficient approach in terms of population numbers at equilibrium compared with those aimed at lanner replacement of peregrine territories (+PL) and lanner colonization of empty territories (+EL). Yet lanner persistence deals with two scenarios, the first involving the application of measures to avoid replacement by peregrines (–LP) and the second measures to avoid territory abandonment by lanners (–LE). This latter (Fig. 2) provides the highest numerical reward in terms of lanner territories occupied in the long term, reversing its population decline, while maintaining an acceptable peregrine population (at the 32% increased level of 2013). A relatively low 5% increase in lanner-to-lanner transition (+LL), compensated by a 5% decrease in the lanner-to-empty transition (–LE), would consequently achieve 60 lanner pairs,

Table 1 Estimated average transition matrix for the lanner falcon *Falco biarmicus feldeggii* and the peregrine falcon *Falco peregrinus brookei* in Sicily (Italy) resulting from territory occupancy state transitions observed between 2000 and 2013

	Time <i>t</i>		
	Lanner	Peregrine	Empty
Time <i>t</i> + 1			
Lanner	95.20% (555) persistence	1.15% (3) replacement	4.35% (13) colonization
Peregrine	1.54% (9) replacement	96.18% (252) persistence	4.35% (13) colonization
Empty	3.26% (19) abandonment	2.67% (7) abandonment	91.30% (273) persistence
Total	100% (583)	100% (262)	100% (299)

Observed frequencies are in parentheses.

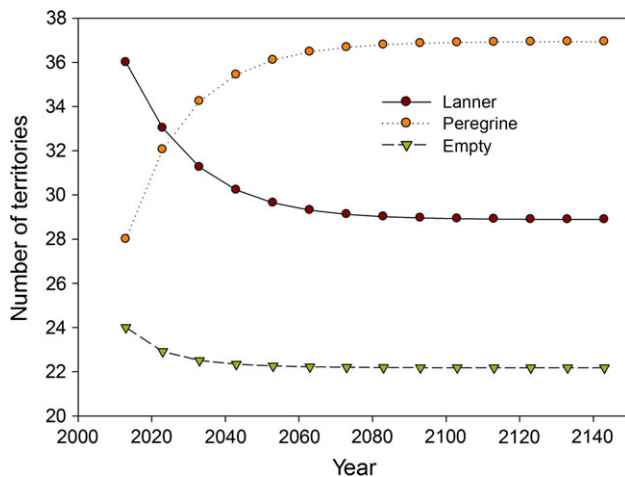


Figure 1 Projected changes in the number of territories occupied by lanner falcon, peregrine falcon and vacant territories in Sicily (Italy) according to the baseline scenario obtained from territory occupancy state transitions observed in 2000–2013.

28 peregrine pairs and 0 empty territories at equilibrium. As shown in Fig. 2, the latter result is a more reasonable figure than that obtained from a 2.5% or 5% increase in lanner persistence (+LL), compensated by a similar decrease in the peregrine replacement (−PL).

Elasticity provides further insight into the population dynamics of our two-species system (Fig. 3). The highest number of lanner territories was reached in a scenario that modelled an increase in persistence probability compensated by a similar decrease in abandonment probability. The second-best option would be to encourage measures aimed at favouring lanner colonization of empty territories compensated by a decrease in the colonization of vacant territories by peregrines. Eventually, the third option aimed at decreasing peregrine persistence in favour of lanner replacement of territories occupied by peregrine, is numerically valid, but ecologically implausible.

Discussion

Here we used a long-term monitoring scheme to provide information on the site-occupation dynamics of two protected top predators. For our system, interactions of these two large falcons were depicted by a four-state MC model (i.e. colonization, abandonment, replacement, persistence), which suggested the absence of temporal variations in the transition rates. Although the concepts of equilibrium occupancy obtained by the process of first-order MCA could be considered rather simplistic to express the complexity of species interactions, it should be remarked that the aim of such demographic analysis is not to forecast the real trajectories of population sizes in the future. In fact, the Markovian statistical tool represents a null model against which to compare the consequences of maintaining indefinitely the current conditions with those of alternative conditions (MacKenzie *et al.*, 2006; Martin *et al.*, 2009b). This gives a relevant heuristic value that greatly increases the potential to respond to ecological questions and conservation problems (Martin *et al.*, 2009a; Miller *et al.*, 2012).

Degree of competition between lanner and peregrine

As expected in members of the same phylogenetic group (Fuchs *et al.*, 2015), Mediterranean populations of peregrine and lanner have very similar body sizes, as occurs for other subspecies such as *F. p. minor* and *F. b. biarmicus* (Jenkins, 1995). Interestingly, the wing area and wing loading, which we could not test in our study and that predict significant differences in the hunting abilities of the two South African falcons (Jenkins, 1995), have size ratios (HRs ≥ 1.3) equivalent to the minimum morphometric spacing necessary for coexistence (Hutchinson, 1959). In addition, Ward, Weigl & Conroy (2002) showed how the biomechanics of the hind limb is important for resource partitioning and habitat coexistence in raptor guilds. Hence, in our study area, despite the large overlap in size, other functional traits of the phenotype could be relaxing competition between the two falcons. Accordingly, niche partitioning, with the lanner laying earlier and choosing different cliffs than peregrines (Amato *et al.*, 2014), seems to support a basic coexistence in Sicily that would be enough to overcome the phylogenetic niche conservatism arising from strong morphological similarities and diet overlap.

Recent range expansion of one species can have negative effects on the occupancy dynamics of congener species (e.g. Dugger, Anthony & Andrews, 2011), as in the case of the expanding population of peregrines in Sicily (Sarà, 2008). This latter species, favoured by anthropogenic habitat alteration, is likely increasing its interference competition with the lanner (Sarà, 2014), thus occupying lanners' cliffs (Di Vittorio *et al.*, 2015). This process could in turn break the species' spatial segregation of habitat during reproduction, and the MCA provided novel information about the occupancy dynamics occurring in the study area. In the observed transition matrix, persistence probabilities were higher than inter-specific transitions, showing that modelled populations would reach a stable-state equilibrium distribution in the long term (year 2065), thereby lending support to a possible future coexistence between the two species despite their actual fluctuating demography. Similar to the data found for large eagles (López-López *et al.*, 2009) and forest raptors (Jiménez-Franco *et al.*, 2011) in Spain, this result would suggest that inter-specific competition currently has a limited role in Mediterranean communities of raptors. Nonetheless, the real influence of inter-specific competition could be masked by anthropogenic factors. For example, human disturbance can drive coexistence by pushing species to less human-populated areas (Moreno-Rueda *et al.*, 2009), or in degraded habitats species may coexist merely because the requirement of vital resources offsets the costs of settling close to a competitor (e.g. Brambilla *et al.*, 2010).

Perturbation analysis and lanner conservation

We modelled three scenarios for each of three transition probabilities of two compensatory variables, yielding 18 sensitivity models, which were further scaled to assess the relative effects

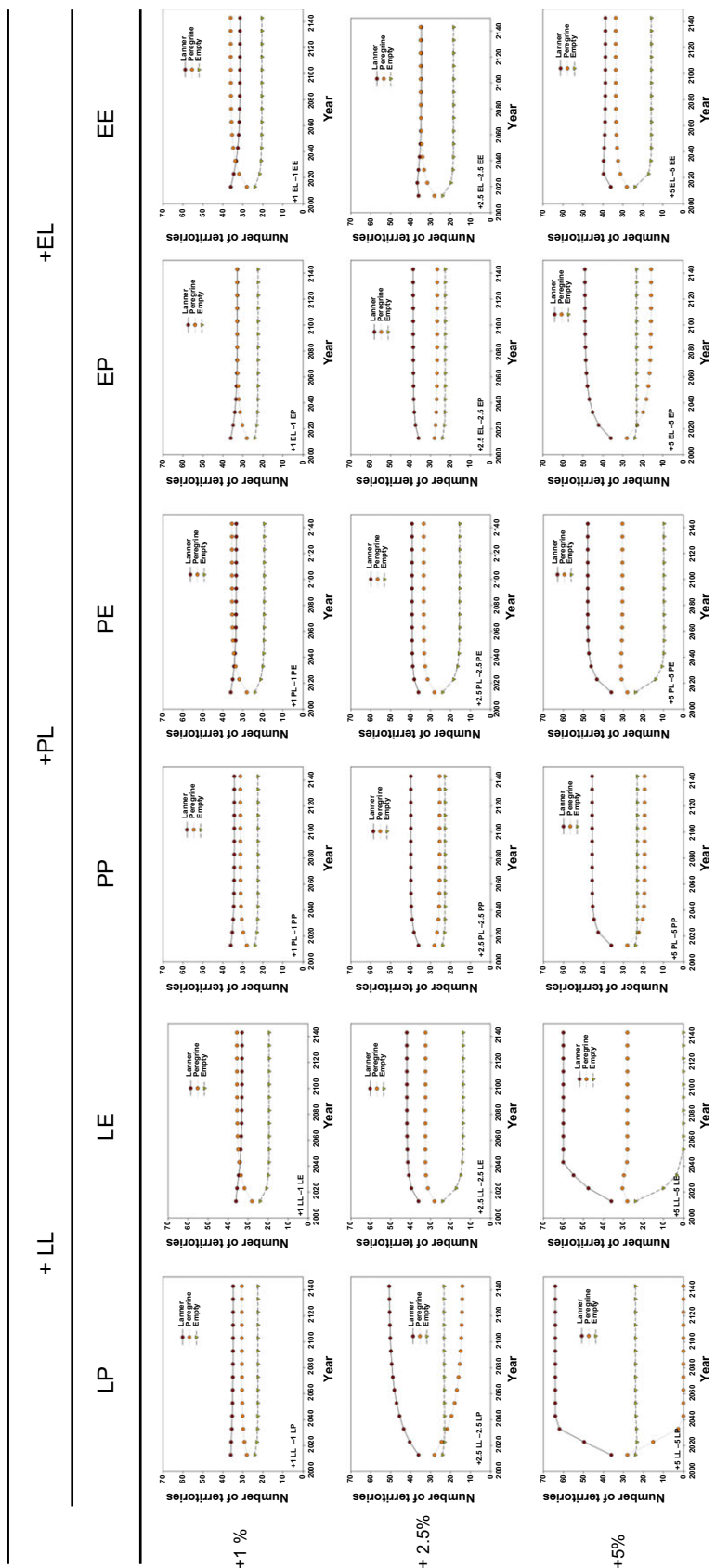


Figure 2 Sensitivity analysis of the Markov chain. Changes were modelled by iteratively increasing the transition probability of the variable of interest to 1, 2.5 and 5% (first row of the heading) and consequently decreasing the compensatory variable (second row of the heading). For example, the upper left figure shows the effect of 1% increase in the transition probability from lanner to lanner compensated by 1% decrease of the transition probability from lanner to peregrine (LP) or to empty (LE). LL reflects measures aimed at favouring persistence, PL shows an increase in replacement from peregrines to lanners, and EL reflects measures aimed at favouring colonization of empty territories by lanners. In every of the 18 models the upper line refers to lanner, the middle to peregrine and the lower to empty sites.

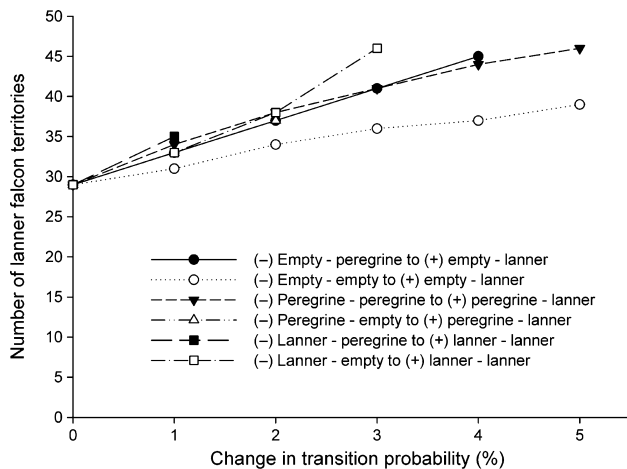


Figure 3 Results of elasticity analysis of the transition matrix of the baseline scenario. The figure shows lanner falcon final population size in Sicily under different scenarios. Increasing the probability of lanner falcon: (1) colonizing empty territories (empty–lanner), (2) replacing territories occupied by peregrines (peregrine–lanner) and (3) persistence of territories (lanner–lanner). Changes in transitions are similar to those in Fig. 2. Symbols (+) and (–) indicate increase or decrease in the corresponding transition probability.

of sensitivity (elasticity) on the transition probabilities to provide valuable information on which conservation action may be best suited to halt the decline in lanners (Hill *et al.*, 2004). Interestingly, we found the equilibrium occupancy of the lanner to be >0.5 , and so the species seems more sensitive to abandonment than to the colonization of local sites (Martin *et al.*, 2009b; Green *et al.*, 2011). Translated into conservation practice, this would suggest choosing management strategies that aim to decrease the abandonment of occupied territories and adult mortality, rather than those aimed at encouraging lanner colonization by improving site quality and/or decreasing juvenile mortality.

For example, by simply managing the 5% of lanner territories to favour site persistence would be enough to reverse the negative population trend in our study area. Besides their poor numerical performances, other options seem unrealistic because it is hard to imagine measures that could encourage lanner colonization of empty sites (+EL), as well as their replacement of peregrine sites (+PL), without benefiting or impeding peregrine persistence at the same time. Actions aimed at decreasing peregrine persistence and colonization would require increasing peregrine abandonment rate and decreasing its population size; obviously, neither is acceptable. In summary, from a conservation point of view, management planned to halt site abandonment of the lanner population is also the best compromise with the protected status of the peregrine.

Measures able to prevent lanner abandonment should be applied at landscape scale, for example by building a network of priority areas in order to halt degradation of the steppe-like habitats by agri-environmental schemes (Sarà, 2014). In addition, management strategies at territory scale should promote

persistence rates favouring territorial fidelity through increasing reproductive success (Sergio & Newton, 2003) and recruitment through proactive actions (Jiménez-Franco *et al.*, 2011), such as (1) minimizing illegal nest predation and preventing human disturbance during the breeding period and (2) reducing unnatural mortality caused by shooting and electrocution of adults during winter and juveniles during post-breeding dispersal.

Conservation implications

In our opinion, the MCA support for coexistence in the long-term should immediately exclude the option of passive conservation, taking into account that our system is framed in fast-changing Mediterranean ecosystems (Sokos *et al.*, 2013). In addition, the insular condition of the populations drives the probabilities of local extinction and colonization (Ferraz *et al.*, 2007) and is expected to influence the occupancy dynamics of the two falcons in synergy with human disturbance. Hence, managers should not simply ‘sit and wait’ for the two species to arrange themselves in a new population equilibrium, because transition probabilities could change over time and then model predictions might vary with respect to the original ones, thus underestimating the real ecological process going on. Considering current or future scenarios, measures aimed at halting lanner decline are urgently needed.

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Supporting Information

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

Table S1. Size overlap test of the Hutchinson's hypothesis about the critical minimum separation necessary for coexistence of lanner and peregrine falcons living in Sicily.

Table S2. Niche overlap test of lanner and peregrine falcons according to the Pianka's index.

Appendix S1. Rationale and computational details for ecological equivalence of lanner and peregrine falcons.