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Life history traits and sensitivity to landscape change: the case of birds and mammals of mediterranean Chile

Rasgos de historia de vida y sensibilidad a los cambios de paisaje: el caso de los mamíferos y aves de Chile mediterráneo

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ABSTRACT

Life history traits may constitute adequate indicators of the sensitivity of a species to changes in habitat/landscape availability. In this study we examine the role of life history traits in the responses of birds and mammals from the mediterranean-climate region of Chile to landscape change. Through a literature survey, we assess an index of sensitivity that may unravel which life history traits induce higher vulnerability to habitat/landscape transformation. Results revealed a broad range of relevant life history traits in mediterranean rodents and birds. Species with high sensitivity indices include *Chelemys megalonyx*, *Octodon bridgesi* and *O. lunatus* among rodents, and *Columba araucana*, *Patagona gigas*, *Campephilus magellanicus*, *Scelorchilus albicollis*, *Scytalopus magellanicus*, *Agelaius thilius*, *Asio flammeus*, and *Strix rufipes*, among birds. Two traits, reproductive effort and habitat requirements, are particularly important for the most sensitive species. The correlation between the sensitivity index and the conservation status of species suggests that the subjective judgments upon which Red Lists are based are supported by biological attributes. However, such listings may overlook some species. The approach reveals that a minimum of biological information can provide useful guidelines to establish criteria for the conservation of Chilean mediterranean mammals and birds.

Key words: birds, central Chile, reproductive effort, habitat, life histories, rodents.

RESUMEN

Los rasgos de historia de vida podrían constituir indicadores adecuados de la sensibilidad de las especies a los cambios en disponibilidad de hábitat/paisaje. En este estudio examinamos el papel de los atributos de historia de vida en la respuesta a los cambios de paisaje de aves y mamíferos de la región mediterránea de Chile. Para ello evaluamos un índice de sensibilidad para determinar qué rasgos de historia de vida producen una mayor vulnerabilidad a las transformaciones del hábitat/paisaje. Los resultados mostraron un amplio rango de atributos de historia de vida relevantes en roedores y aves de la zona mediterránea. Entre las especies con altos índices de sensibilidad se encontraron los roedores *Chelemys megalonyx*, *Octodon bridgesi* y *O. lunatus*, y las aves *Columba araucana*, *Patagona gigas*, *Campephilus magellanicus*, *Scelorchilus albicollis*, *Scytalopus magellanicus*, *Agelaius thilius*, *Asio flammeus*, y *Strix rufipes*. Esfuerzo reproductivo y requerimientos de hábitat son los atributos más importantes en las especies más sensibles. La correlación entre el índice de sensibilidad y el status de conservación de las especies sugiere que los juicios subjetivos sobre los cuales se basan los Libros Rojos se apoyan en atributos biológicos. Sin embargo, tales listados pueden pasar por alto algunas especies. La aproximación descrita muestra que un mínimo de información biológica puede proveer de útiles directrices para establecer criterios en la conservación de mamíferos y aves de Chile mediterráneo.

Palabras clave: aves, Chile central, esfuerzo reproductivo, hábitat, historias de vida, roedores.

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INTRODUCTION

Landscape modification, mainly caused by humans, is the most common threat to species survival. Habitat loss, fragmentation and degradation usually trigger population declines, increasing the probability of a species' local and global extinction (Groom & Schumaker 1993, Fahrig & Grez 1996). Anthropogenic land changes account for 35% of contemporary animal extinctions for which causes are known. Similarly, 76% of threatened mammals are menaced by habitat destruction (Groombridge 1992). Land-use patterns are likely to intensify in the next decades (Leemans & Zuidema 1995). Consequently, criteria and indices to predict species sensitivity to landscape changes are badly needed to predict which species might be more prone to extinction.

From all phenotypic features of an organism, life history traits, being closely linked to fitness (Mousseau & Roff 1987, Roff 1997), are particularly sensitive to selective pressures, and hence to ecological changes (Stearns 1992). Life history traits have low heritability compared to other phenotypic traits (Roff 1992, 1997, Stearns 1992), and therefore may respond more rapidly to selection (Charlesworth 1994, Falconer & Mackay 1996, Roff 1997, but see Price & Schluter 1991). Ecological changes derived from landscape modifications might favour different life histories through their differential effects on reproduction, and mortality (Southwood 1977, 1988, Stearns 1992). Therefore, an analysis of life history traits, such as reproductive effort and habitat requirements, may suggest what set of attributes render a species more vulnerable to landscape change (Hansen & Urban 1992). This approach offers an alternative method to understand and predict the conservation status of species compared to the currently subjective judgments upon which most Red Lists are based (Mace 1995). By landscape change we consider habitat loss or fragmentation caused by human activities, and with an overall reduction in the amount and quality of habitat (Forman 1995).

Mediterranean evergreen shrublands are among the most disturbed and threatened biomes worldwide (Hannah et al. 1995). Mediterranean regions harbor a remarkably high biodiversity (Cowling et al. 1996); they are considered "hot-spots" precisely due to their high and unique biological richness and their intense land use, demanding urgent protection (Myers 1990). The mediterranean-climate region of Chile is no exception. It has been subjected to anthropogenic landscape changes for millennia (Fuentes 1990). This region supports a rich and diverse biota, a fraction of which either has locally vanished or face extirpation (Miller 1980, Simonetti & Cornejo 1990, Arroyo et al. 1995, Simonetti 1999, Cofré & Marquet 1999). Several mediterranean species are included in the Chilean Red List, a recognition of their threatened status (Glade 1993). However, there are no ecological comparative analyses of the biological attributes that could be underpinning their status (but see Jaksic & Jiménez 1986 for Chilean raptors).

In this paper we examine the role of life history traits in the responses of birds and mammals from the mediterranean-climate region of Chile to landscape change. Following the sensitivity index proposed by Hansen & Urban (1992) for North American bird assemblages, we aim to identify specific traits or suites of traits that contribute more significantly to species endangerment when facing landscape modifications. Second, we compare the ranking of species' sensitivity to their current conservation status in the Chilean Red List. Congruency between the sensitivity index and their conservation status will validate such listings.

MATERIAL AND METHODS

Following Hansen & Urban (1992), we use a comprehensive definition of life history, including traits related to reproductive strategy, space utilization, and habitat requirements (see also O'Connor 1985, Sibly & Calow 1985, Roff 1992). We assessed the potential responsiveness of species to landscape modification through a sensitivity index (SI) based on six life history traits: reproductive effort (litter size times the annual number of reproductive events), type of nest or den, nest/den position, space use or abundance, habitat requirements, and migratory behavior (Table 1). These traits comprehend a range of life history atributes that include several aspects of the organismal biology of the animals, from reproductive success to resource utilization. By type of nest/den we refer to whether animals use holes and/or covered cavities in trees or soil (low vulnerability), use cup like semi-open nests/dens (intermediate vulnerability), or use open barely hollow nest/den (high vulnerability). Nest/den position represents the height from the ground (>3 m, low vulnerability; 1-3 m, intermediate; < 1 m high). In relation to migratory behavior, it has been suggested that those species mosts vulnerable to landscape modifications are those animals with reproductive migrations, since the lack of a habitat may generates a failed migration with no reproduction, particularly since migration interacts with other life history traits (O'Connor 1985, Hansen & Urban 1992, Sutherland & Dolman 1994). Resident non-migrant species would be least sensitive to land transformations, whereas animals with short non-reproductive migrations (e.g., long-term traplining birds) would have an intermediate sensitive to landscape change (O'Connor 1985, Hansen & Urban 1992). Each trait could range from 1 (least sensitive) to 3 (most sensitive) depending on its value or status (Hansen & Urban 1992; Table 1). The SI for a species is obtained by summing the scores across traits. The higher the value, the more sensitive the species is to landscape change. This approach assumes that life history traits have little or no variance. While this assumption may not be entirely correct (McNamara & Houston 1996, Roff 1997), life history traits are more variable between than within species, supporting inter-specific comparisons (Roff 1992, Stearns 1992).

Rather than embracing an exhaustive review of the fauna from the mediterranean region of Chile, we aim to exemplify the heuristic value of this approach focusing on a suite of species. We selected 21 bird and 11 mammal species belonging to 9 different families (6 avian and 3 mammalian), largely based on information availability. From this selected families we assessed those species that inhabit the mediterranean-climate region of central Chile, including some species that at present time

TABLE 1

Life history criteria used to rate the sensitivity (1 = least sensitive; 3 = most sensitive) of bird and mammal species to landscape change. The overall index value for a particular species is the summation of individual values across life history traits (see Material and Methods)

Criterios de historia de vida usados para categorizar la sensibilidad (1 = menos sensible; 3 = más sensible) de especies de aves y roedores a los cambios de paisaje. El valor global del índice para una especie particular es la suma de los valores individuales de cada rasgo de historia de vida (véase Material y Métodos)

	Sensitivity score		
Life history traits	1	2	3
reproductive effort (litter size/year)	> 10	6 - 10	0 - 5
nest/den form	hole	semi-open	open
nest/den height (m)	> 3	1 - 3	< 1
space use or abundance	abundant	intermediate	rare
habitat requirements	generalist	closed-canopy, open-canopy	old growth
migratory behavior	resident	short	long or reproductive

TABLE 2

Sensitivity to landscape change of (a) rodent and (b) bird species of mediterranean Chile. Higher values of the index indicate greater sensitivity. Those species with conservation status in central Chile (according to Glade 1993) are also indicated (- = without status; K = insufficiently known; I = indeterminate; V = vulnerable; E = endangered)

Sensibilidad a los cambios de paisaje de (a) roedores, y (b) aves de Chile mediterráneo. Valores mayores del índice indican mayor sensibilidad. Se indican también aquellas especies con alguna categoría de conservación para Chile central (según Glade 1993; - = no categorizada; K = insuficientemente conocida; I = indeterminada; V = vulnerable; E = en peligro)

Taxa	Family	Species	Sensitivity index	Conservation status
(a) Rodents				
	Muridae			
		Abrothrix longipilis	12	K
		Abrothrix olivaceus	10	-
		Chelemys megalonyx	14	E
		Euneomys chinchilloides	13	K
		Oligoryzomys longicaudatus	9	-
		Phyllotis darwini	11	-
	Octodontidae			
		Octodon degus	10	-
		Octodon bridgesi	14	V
		Octodon lunatus	14	V
		Spalacopus cyanus	12	-
	Abrocomidae			
		Abrocoma bennetti	11	I
(b) Birds				
	Columbidae			
		Columba araucana	15	E
		Zenaida auriculata	11	-
		Columbina picui	12	-
	Trochilidae			
		Patagona gigas	14	-
		Sephanoides sephaniodes	12	-
	Picidae			
		Colaptes pitius	11	-
		Picoides lignarius	11	-
		Campephilus magellanicus	14	E
	Rhinocryptidae			
		Pteroptochos castaneus	13	-
		Pteroptochos megapodius	13	-
		Scelorchilus albicollis	14	-
		Scytalopus magellanicus	14	-
	Icterinae			
		Molothrus bonariensis	11	-
		Curaeus curaeus	13	-
		Agelaius thilius	14	-
		Sturnella loyca	13	-
	Strigidae			
		Bubo virginianus	11	-
		Glaucidium nanum	10	-
		Asio flammeus	14	K
		Athene cunicularia	11	-
		Strix rufipes	14	K

occupy marginal areas of this region (e.g., *Campephilus magellanicus*). Our selection of families included species with disparate amounts of available information and conservation status. Therefore, the sample should be representative of any broader taxonomic analysis. Life history information was obtained through a perusal of the literature. Most of the data were obtained from Johnson (1965, 1967) for birds, and from Redford & Eisenberg (1992), and Mann (1978) for mammals, supplemented by works by Glanz (1977), Meserve & Le Boulengé (1987), and Meserve et al. (1996) for mammals, and Schlatter (1979), Jaksic & Jiménez (1986), Estades (1995), and Martínez & Jaksic (1996) for birds. Although the quality of this information is somewhat variable (owing to different sample sizes, recording methodologies, and observers, among other factors), to our knowledge, the data is the best available and sufficiently reliable to exemplify the approach. In the few cases when available information was ambiguous or scarce for a given trait, we used the value of the closest relative species with the lowest index value for that trait. Therefore, if anything, our analysis may underestimates the sensitivity to landscape change.

The outcome of the SI was compared to the ranking of each species in the Red List of Chilean vertebrates (Glade 1993). A nonparametric correlation between the index and conservation ranking was performed. The conservation status of each species in central Chile was ranked as follows: without status (i.e., unthreatened species not included in the Red List) = 1; out of danger = 2; status not defined, insufficiently known, and indeterminate = 3; rare = 4; vulnerable = 5; endangered = 6; and extinct = 7.

RESULTS

Mediterranean birds and mammals of Chile exhibit an extensive range of life history traits, with sensitivity index values from SI = 9 (of a possible minimum of 6) in the long-tailed rice rat (*Oligoryzomys longicaudatus* Bennett, 1832) to SI = 15 (of a possible maximum of 18) in the Chilean pigeon (*Columba araucana* Lesson, 1827; Table 2). Among rodents, the murid *Chelemys megalonyx* (Waterhouse, 1845) and the octodontids *Octodon bridgesi* (Waterhouse, 1845) and *O. lunatus* (Osgood, 1943) show the highest sensitivity (SI = 14), while the long-tailed rice rat (*O. longicaudatus*), the olivaceus field mouse (*Abrothrix olivaceus* Waterhouse, 1837), the leaf-eared mouse (*Phyllotis darwini* Waterhouse, 1837), and the degu (*Octodon degus* Molina, 1782) are the least sensitive to landscape change (Table 2a).

Among birds, the Chilean pigeon (*C. araucana*) appears as the most sensitive species (SI = 15) closely followed by the Giant hummingbird (*Patagona gigas* Vieillot, 1824), the Magellanic woodpecker

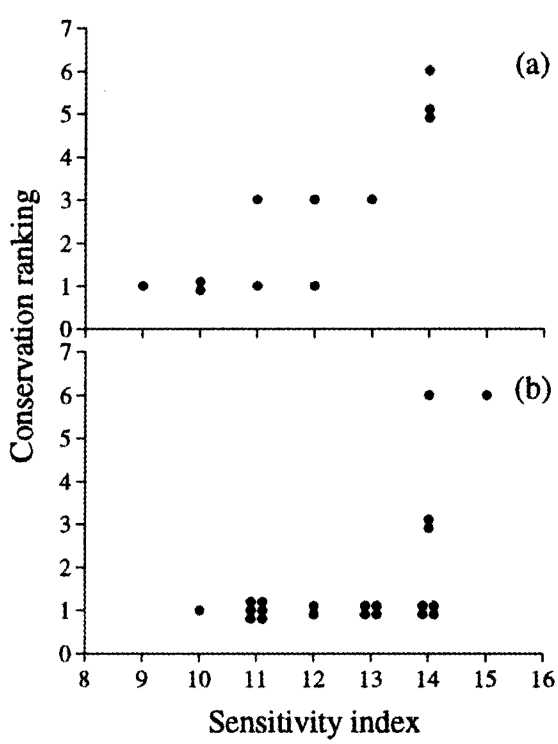

Fig. 1. Correlation between sensitivity index and conservation ranking for (a) rodents, and (b) birds. Each point represents one species. Statistical analyses in the text.

Correlación entre índice de sensibilidad y nivel de conservación para (a) roedores y (b) aves. Cada punto representa una especie. Análisis estadístico en el texto.

(*Campephilus magellanicus* King, 1828), the White-throated tapaculo (*Scelorchilus albicollis* Kittlitz, 1830), the Andean tapaculo (*Scytalopus magellanicus* Gmelin, 1789), the Yellow-winged blackbird (*Agelaius thilius* Molina, 1782), and two strigiforms, the Short-eared owl (*Asio flammeus* Pontoppidan, 1763), and the Rufous-legged owl (*Strix rufipes* King, 1828), all with SI = 14 (Table 2b). Avian species with low sensitivity to landscape change comprise the Eared dove (*Zenaida auriculata* des Murs, 1847), the Chilean flicker (*Colaptes pitius* Molina, 1782), the Striped woodpecker (*Picoides lignarius* Molina, 1782), the Shiny cowbird (*Molothrus bonariensis* Gmelin, 1789), the Great horned owl (*Bubo virginianus* Gmelin, 1788), the Austral pygmy owl (*Glaucidium nanum* King, 1828), and the Burrowing owl (*Athene cunicularia* Molina, 1782) (Table 2b).

In general, for the species most sensitive to habitat modification, two life history traits were particularly important: reproductive effort, and habitat requirements. Among the 11 species with SI ≥ 14, 73% have maximum scores in reproductive effort and habitat requirements, while among the four species with SI ≤ 10, only one species has maximum score in reproductive effort and none in habitat requirements.

The SI of both birds and mammals were significantly correlated with their rankings in the Chilean Red List (Spearman corrected for ties, $r_s = 0.86$, $P = 0.006$ for rodents; $r_s = 0.59$, $P = 0.009$, for birds; see Fig. 1), although there was a large deviance in the bird data, in particular for the lowest conservation rank (Fig. 1b).

DISCUSSION

Habitat specialization and low reproductive effort increase extinction probability (Gilpin & Soulé 1986). In fact, those life history traits were the most significant in determining the sensitivity of central Chilean species to landscape change. While this result is not surprising, its covariation and the comparatively minor effect of the other traits, offer a guideline when selecting species for conservation efforts.

The four most sensitive species to landscape modifications require old growth forest or dense vegetation, the habitat which has been disappearing from central Chile. Among them, a paradoxical case is *O. bridgesi*, listed as Vulnerable in the Red List, but considered a pest in some commercial forests (Rodríguez 1993). Inhabitant of dense vegetation, *O. bridgesi* might use the dense understory of young plantations as an alternative habitat that could compensate the loss of natural habitat. However, this species is being controlled by poisoning, habitat modification, and predator manipulations (Murúa & Rodríguez 1989, Muñoz & Murúa 1990). The reliance of *O. bridgesi* on disappearing dense woodlands is implied by its extinction from several localities in central Chile since precolumbian times (Simonetti & Saavedra 1998).

The sensitivity of the Chilean pigeon (*C. araucana*) is primarily due also to habitat requirements (mainly old growth), low reproductive success (1-2 broods per year), and its vulnerable open nesting. Johnson (1967) stated that the Chilean pigeon nests "are mere rudimentary platforms of twigs with the light showing through in all directions". Similarly, other avian species sensitive to landscape changes, such as rhinocryptids, also require old growth forests and have low reproductive efforts. It is not surprising then, that the Magellanic woodpecker (*C. magellanicus*) shows a high SI, since it inhabits old growth forests and currently its distribution is limited to the southern boundary of the mediterranean-climate region (Araya & Millie 1988). Restricting the analysis for the same life history traits, the Rufous-legged owl (*S. rufipes*) shows the same SI as its North American relative, the Spotted owl (*S. occidentalis*; see Hanson & Urban 1992); both species are well known for their old growth forest requirements (Martínez & Jaksic 1996).

Three bird species, the Giant hummingbird (*P. gigas*), the Yellow-winged blackbird (*A. thilius*), and the Short-eared owl (*A. flammeus*), show counterintuitive results. They have high indexes of sensitivity to landscape change despite inhabiting open canopy habitats, which is the habitat increased by landclearing. However, these three species have very small clutch sizes and open nests. Further, the giant hummingbird is a reproductive migrant, and the yellow-winged blackbird and the short-eared owl nest on (or very close to) the ground, variables that increase their vulnerability to trampling, parasitism, and predation. Observational and experimental evidence shows that local predators are conspicuous egg consumers (Lazo & Anabalón 1992, Bresciano et al. 1999).

Habitat specialization increases the sensitivity of birds and mammals in mediterranean Chile, which agrees with the reputed most common cause of species endangerment in the region: habitat disturbance. Habitat alteration, largely woodland reduction, accounts for a higher proportion of threatened species than in other parts of the country. Such reduction has been associated to the high intensity of the human occupation of the area (Miller 1980, Simonetti 1999). A reduction in woodlands however, might also increase the area suitable for open canopy dwellers and habitat generalists. Species such as the olivaceus field mouse (*A. olivaceus*) and the degu (*O. degus*) are most common in open shrublands (Glanz 1977, 1984). Their current abundance in central Chile might be a by-product of anthropogenic land use (Simonetti 1989a). None of these species is included in the Red List of Chilean vertebrates, but often they are regarded as pests (Rodríguez 1993).

The sensitivity index, derived independently from any assessment of conservation status, agrees well with the rank of vulnerability derived from the Red List of Chilean vertebrates (see Glade 1993). Although the Red List information does not focus on landscape or habitat modification explicitly, the listing is expected to be indicative of the degree of species sensitivity to any kind of anthropogenic perturbation, including landscape changes. The correspondence between SI and the conservation status strongly suggests that criteria, albeit unstated, used to include species in the Red List are correlated with biological attributes of the species considered. If anything, the Red List fails by being too conservative. While rodent species with high SI were also those species with recognized problems of conservation, several bird species previously considered with no conservation problems according to the Red List (see Glade 1993), had high SI. These avian species included the Giant hummingbird (*P. gigas*), the Yellow-winged blackbird (*A. thilius*), and two rhinocryptids, the White-throated tapaculo (*S. albicolis*), and the Andean tapaculo (*S. magellanicus*). They are all characterized by low reproductive effort, and open nesting behavior (with the exception of *S. albicolis*). Therefore, unless using a more objective, biologically explicit criteria, the Red List can overlook possible conservation problems in species intuitively considered as resistant to disturbance.The sensitivity index can assist specialists in defining species of conservation concern.

The simple sensitivity index used here, after Hansen & Urban (1992), exemplifies that a minimum of biological information about species can provide useful guidelines for the conservation of mediterranean mammals and birds of Chile. Although quantitative genetic studies show that life history traits are more closely linked to fitness than morphological and behavioral traits (Mousseau & Roff 1987, Stearns 1992, Roff 1997), we believe the approach could be extended to include the latter, in particular when there is evidence of conspicuous differences between species, as it is the case of birds (Cody 1974) and rodents (Simonetti 1989b, Vásquez 1996) from central Chile. We support the common plea (e.g., Jaksic & Simonetti 1987) of the need to obtain more detailed information on different aspects of species' life history, read natural history, for accurate determination of the actual and potential effects of landscape transformation on species survival, and hence to protect the biological richness of mediterranean ecosystems.

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