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METAPOPULATION APPROACH TO ASSESS SURVIVAL OF *ONCIFELIS GUIGNA* IN FRAGMENTED FORESTS OF CENTRAL CHILE: A THEORETICAL MODEL

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ABSTRACT. Habitat loss and fragmentation have been identified as the main threats to the survival of the kodkod, *Oncifelis guigna,* an endangered felid endemic to the temperate forests of southern Chile and Argentina. In Chile *O. guigna* is considered endangered, and is restricted to native forests. The continuing reduction and fragmentation of these forests, particularly in the coastal mountain chain of central Chile, constitutes a threat to its survival. In a theoretical exercise we employ a metapopulation approach to infer probability of maintenance of protected populations of *O. guigna* in national parks and reserves of the coastal zone of central Chile between 35º 30' and 38º S. We used the S. Harrison classification to determine the type of metapopulation depending on the size and degree of isolation of existing populations in the forest fragments. Thus, we identified 11 potential metapopulations, of which eight would be in non-equilibrium state (extinct or near extinction), one mainland-island type and two that were unclassified. One metapopulation located within the Nahuelbuta National Park is surrounded by native forest fragments and was deemed viable in the long-term. On the other hand, another metapopulation, composed of Los Queules and Los Ruiles National Reserves, could be maintained if an active conservation program is established to protect the native forest fragments surrounding them; otherwise this population will also tend to extinction. Through this model we may infer that *O. guigna* populations in central Chile would require the preservation of small native forest fragments placed outside protected areas. Finally, we point out the necessity for further field research on this species to calibrate our model.

RESUMEN: Aproximación metapoblacional para determinar la sobrevivencia de *Oncifelis guigna* en bosques frragmentados de Chile central: un modelo teórico. La pérdida y fragmentación de hábitat han sido identificados como las principales amenazas para la sobrevivencia de *Oncifelis guigna,* felino endémico de los bosques templados del sur de Chile y Argentina. Esta especie ha sido descrita como restringida a estos bosques nativos. La creciente reducción y fragmentación de este hábitat, especialmente en la cordillera de la costa en Chile central, constituye una amenaza a su sobrevivencia. Actualmente, *O. guigna* es considerado en peligro de extinción en Chile. En un ejercicio teórico utilizamos una aproximación metapoblacional para inferir la probabilidad de extinción de las poblaciones protegidas en parques y reservas de la zona costera de Chile central entre los 35º 30' y 38º S. Empleamos la tipificación de S. Harrison para determinar el tipo de metapoblación dependiendo del tamaño y grado de aislamiento de las poblaciones existentes en los fragmentos de bosques. De este modo, identificamos que existirían 11 potencia-

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les metapoblaciones, de las cuales ocho serían metapoblaciones en no-equilibrio (extintas o cercanas a la extinción), una del tipo continente-isla y dos no serían clasificables según la metodología empleada. La única metapoblación viable en la actualidad correspondería a la del Parque Nacional Nahuelbuta, la cual incluye los fragmentos remanentes vecinos al parque. Por otra parte, la otra metapoblación compuesta por las Reservas Nacionales Los Queules y Los Ruiles podría mantenerse si se instalara un activo plan de protección de los fragmentos aledaños a éstas. Sin ellos, ambas poblaciones tenderían a la extinción tarde o temprano. Mediante este modelo, podemos inferir que las poblaciones de *O. guigna* en la zona central requerirían de la mantención de los pequeños fragmentos de bosque nativo ubicados fuera de las áreas silvestres protegidas. Finalmente hacemos hincapié en la necesidad de obtener más datos de la biología de esta especie para calibrar nuestro modelo.

Key words: conservation, central Chile, forest fragmentation, kodkod, metapopulation, *Oncifelis guigna.*

Palabras clave: conservación, Chile central, fragmentación de bosques, güiña, metapoblaciones, *Oncifelis guigna*.

INTRODUCTION

The kodkod *Oncifelis guigna* (**Fig. 1**), the smallest wild felid in South America, has a restricted geographical distribution in central and southern Chile and adjacent Andean regions of Argentina (Redford and Eisenberg, 1992). In Chile, its historic distribution ranges from 33º to 50º S (including Chiloé Island and the Guaitecas Peninsula), where it inhabits temperate forests (Greer, 1965). *O. guigna* is one of the two most threatened wild cats in South America (Nowell and Jackson, 1996), mainly due to its close association with native forests (e.g. *Nothofagus* spp.) (Nowell and Jackson, 1996), which are suffering increasing fragmentation and encroachment from agro-forestry operations.

Although *O. guigna* was considered fairly common as late as the early 1960's (Osgood, 1943; Greer, 1965), it is currently regarded as endangered in Chile and vulnerable in Argentina (Glade, 1988; Díaz and Ojeda, 2000) and is listed on Appendix II of (CITES) and its conservation status is considered as Vulnerable (VU C2a) by IUCN (2002).

The primary threats to *O. guigna* populations are habitat destruction and human persecution, particularly in central Chile (Miller et al., 1983). In fact, the replacement of native forest with coniferous (*Pinus radiata*) plantations has been particularly extensive in the forests of the coastal range of central Chile, where up to 31% of the native forest was replaced during the period 1978-1987 (Donoso and Lara, 1996). In recent years, native forests in the Maule region have been further reduced and fragmented (Grez et al., 1997; Bustamante and Castor, 1998).

In Chile, *O. guigna* populations have been recorded in 16 national parks and reserves (unpublished data). However, it is not known whether these parks are large enough to sustain viable populations. Simonetti and Mella (1997) in a theoretical analysis have found that, in terms of park size, only 45% of Chilean protected areas are likely to be large enough to ensure the long-term persistence of many carnivores species, depending on park size and its calculated density e.g., foxes *Pseudalopex culpaeus* and *P. griseus*, skunks *Conepatus humboldtii*, Geoffroy's cat *Oncifelis geoffroyii* and pumas, *Puma concolor*. The remaining parks are unlikely to be capable of sustaining viable populations and local extinction may be expected for carnivores in these protected areas. Parks located in central and southern Chile would sustain the largest losses (Simonetti and Mella, 1997; Simonetti, 1999). Whether the populations of *O. guigna* could follow the same fate is currently unknown.

In a field study Acosta and Simonetti (in press) found that *O. guigna* preferred native forest to pine plantations, attributing this selection to differences in vegetation structures and landscape features. Thus, pine plantations

Fig. 1. *Oncifelis guigna* the smallest wild felid in South America (Photo by G. Acosta).

were used depending its distance to a native forest of large size (more than 6 km^2). According to these data we think that *O. guigna* abundance is dependent on the existence of native forest, and that it is more likely to be found in forested areas within parks and forest remnants outside protected areas. Pine plantations or other habitats could be used by *O. guigna* as corridors along which to disperse to other native forests patches. Thus, populations inhabiting large forest blocks within protected areas, along with those thriving in adjacent forest fragments surrounded by a matrix of pine plantations can be considered as metapopulations according to Harrison's criteria (1991).

We employed a metapopulation approach to formulate hypothesis concerning the long-term viability of *O. guigna* in the fragmented forests of central Chile and propose a theoretical approach to assess the viability of *O. guigna* persisting in fragmented forests of central Chile. To do this, we employed both empirical and theoretical data. Thus, firstly we estimate potential population size based on population densities reported in the literature and relate this to patch sizes of forest fragments, assuming that all native forest are available for use. Secondly, we assess connectivity between subpopulations (Taylor et al., 1993) in terms of dispersal ability based on the maximal distance of movement reported for *O. guigna* (Sanderson, pers. comm.) and from mean dispersal distance reported for another wild cat (Sweanor et al., 2000). We then classify metapopulation types using Harrison's (1991) scheme. Lastly, we modeled the metapopulation dynamics following a twenty-year period of extraction of native forest according to current deforestation rates. Finally we discuss the conservation prospects for this small rare felid and make recommendations to ensure its long-term survival in a fragmented landscape.

METHODS

Metapopulation approach

To create our model we first define some concepts in the context of our study. **Subpopulation** will be described as the population of animals connected by their individual home ranges and **Metapopulation** will be the group of subpopulations connected by individuals that disperse from these home ranges. Thus, four metapopulation types have been suggested based on patch size and degree of isolation (Harrison, 1991). In this context and in practical terms, we will define size of native forest patches as synonymous with population size, and hence with the probability of extinction (MacArthur and Wilson, 1967). Therefore, larger patches should offer more resources, thus allowing for larger populations and hence reducing the risk of extinction. Isolation can be caused by large inter-patch distances beyond the dispersal capability of the species, and/or due to the presence of barriers to dispersion such as unsuitable, or less utilized habitat (e.g. crop fields, ice fields, rivers). Populations inhabiting small isolated patches will have higher extinction probabilities and a reduced likelihood to be rescued by immigrants (Gotelli, 1991; Harrison, 1991).

A combination of patch size (large-small) and degree of isolation (isolated-connected) generates, among others, four basic metapopulation types: a) the **"classical metapopulation"**, consisting of a group of small habitat patches (subpopulations) that are extinction-prone due to their small size, but which are located sufficiently close to other subpopulations for recolonization to occur; b) the **"patchy metapopulation"**, comprising a set of small patches which are located so close as to behave as a single and large population; c) the **"mainland-island metapopulation"**, which is determined by a large patch and a variable number of small patches, the large patch acting as a propagating source to separated island sub-populations that are close enough to prevent local extinction by providing a continuous source of immigrants, and d) the **"non-equilibrium metapopulation"** consisting of several small and isolated patches, each acting independently and consequently being risk-prone due to their small sizes (see Harrison, 1991).

We classified the metapopulation structure of *O. guigna* in central Chile according to Harrison's (1991) scheme using data from the literature, including a) the distribution of native forest patch sizes as an index of habitat availability, b) movement capability of *O. guigna* to determine patch connectivity and, c) population size, as an indicator of the long-term viability.

Forest availability was assessed from vegetation maps obtained from the Catastro del Bosque Nativo (CONAF, CONAMA, BIRF, 1997). The distribution and abundance of native forest tracts between 35º 30' to 38º S was assessed from maps by plotting native forests and the surrounding matrix (scale 1:500.000). Four protected areas are located in this zone, Nahuelbuta National Park (NP) (Marín, 1969: 69 km^2), Los Queules National Reserve (NR) (CONAF, 1999: 1.5 km^2), Los Ruiles NR (1.5 km^2) and, Los Ruiles sector el Fin (0.2 km^2) (Villa, pers. comm). We assumed that all areas of native forest potentially provide suitable habitat for *O. guigna* (e.g. Lahaye et al., 1994; Simonetti and Mella, 1997). This is a conservative assumption from the viewpoint of kodkod survivorship, as it does not consider edge effects or the successional stage of forest fragments.

The size of *O. guigna* population inhabiting each forest tract or fragment was estimated from population density as reported in the literature (Bowers and Matter, 1997). Recent radiotelemetry studies in Southern Chile suggest that densities of *O. guigna* range from 0.97 to 3.3 individuals/km^2 in protected areas (San Rafael National Park and Queulat National Park respectively; Dunstone et al., 2002a). In this study, we use minimum density population determined on Laguna San Rafael National Park (0.97 individual/ km^2: see Dunstone et al., 2002a) as a conservative value, because of the lack of data for our study region.

To calculate the potential for movement between subpopulations, we assessed the average distance travelled by *O. guigna* from the geometric centre of a home range to its outermost limit from available data (mean home range area 2.25 km^2: Dunstone et al., 2002a; Sanderson et al., 2002). Thus, we used a subpopulation limit of 2.25 km^2. To determine metapopulations, we employed a buffer zone of 7.5 km around the forest patches, assessed as the average daily distance travelled by an individual (i.e., Gros and Rejmánek, 1999) in a highly fragmented environment (Sanderson, pers. comm.) and a theoretical value of 11 km calculated from 7 home range diameter, which was obtained by Sweanor et al. (2000) as a proportion from the dispersal distance with home range diameters in puma. Following Harrison (1991), we considered patches to be connected and acting as a metapopulation, if they were ≤7.5 km apart. Furthermore, we considered the existence of barriers such as rivers (i.e., Biobío river) as an additional variable to influence connectivity and likely to delimit metapopulations.

We used Stith's et al. (1996) criteria to classify subpopulations and metapopulations, depending on patch size and isolation and the extent of suitable habitat available for *O. guigna*. Following a previous study on puma (Beier, 1993), we set the lower limit of the smallest population of 70 animals which he considered adequate to maintain a viable population in the short-term, and we considered 500 animals to delimit largest population which could be viable in a long-term (Frankel and Soulé, 1981; Newmark, 1985; Simonetti and Mella, 1997). Following Harrison (1991) we classified subpopulations as small patches when the available forest area allowed for less than 70 animals, medium sized when subpopulations could reach between 70 and 500 animals, and large if the area was sufficient to support 500 or more individuals. Forest patches unable to contain a single animal were eliminated from our analyses.

Additionally, we modelled the future metapopulation structures and hence the fate of *O. guigna* in central coastal Chile considering a 1.6% annual rate of deforestation (PAF, 1992), leading to a reduction of 30% of native forest over a twenty year period. Thus, our model removed at random the 30% of smallest (<10 ha) and privately owned native forest fragments, which are therefore, prone to deforestation and unlikely to persist in the long-term.

RESULTS

Based on a 7.5 km interpatch distance to delimit metapopulation we calculate that twenty-four subpopulations of *O. guigna* exist in central coastal Chile from 35º 30' to 38º S (**Fig. 2**). Of these, 22 (90%) are likely to hold fewer than 70 individuals, and 13 (55%) less than 10 individuals. Only one subpopulation was large enough to sustain 500 or more individuals (**Fig. 3**). Eleven distinct metapopulations were determined, with 9 (82%) likely to hold fewer than 70 individuals (**Figs. 2** and **3a**). Of these, eight conform to the "non-equilibrium" type, due to the small size of the component forest patches and large interpatch distances (**Table 1**).

Two other metapopulations (including Los Queules and Los Ruiles National Reserve) do not fulfil Harrison's scheme (1991), as they comprise medium sized areas surrounded by two or four forest patches, respectively (**Fig. 3b**). Los Ruiles sector El Fin is defined as a non-equilibrium metapopulation. Only one metapopulation was classified as a "mainland-island" system (Nahuelbuta NP), being comprised of a large native forest tract surrounded by nine small native forest patches, and likely to sustain more than 900 individuals (**Fig. 3b** and **Table 1**).

The simulated 30% reduction in small private owned native forest fragments over a twenty year period using the current deforestation rate showed that *O. guigna* metapopulations declined, leaving only one long-term metapopulation of an estimated 1200 individuals within Nahuelbuta NP and surrounding fragments, and one smaller population (250 individuals) in the Los Queules-Los Ruiles National Reserves metapopulation. Nevertheless, neither Nahuelbuta nor the northern metapopulation would be sufficiently large to maintain themselves in the long-term and only the Nahuelbuta NP population was likely to survive in the short-medium term (almost 70 individuals) due to the reduced area of native forest under protection (see **Figs. 3** and **4**). Furthermore, a reduction of forest fragments and an increase in interfragment distance was observed, creating a new non-equilibrium metapopulation in Los Ruiles National Reserve (**Fig. 4**).

When we employed then a dispersal distance of 11 km through pine plantations, this resulted in some changes to metapopulation configuration. Of the original eleven metapopulation delimited using the 7.5 km criterion, only three remained, of which none fell within the non-equilibrium category when patch extraction was conducted. Of these, the Nahuelbuta metapopulation was retained as a mainland-island category. The northern metapopulation

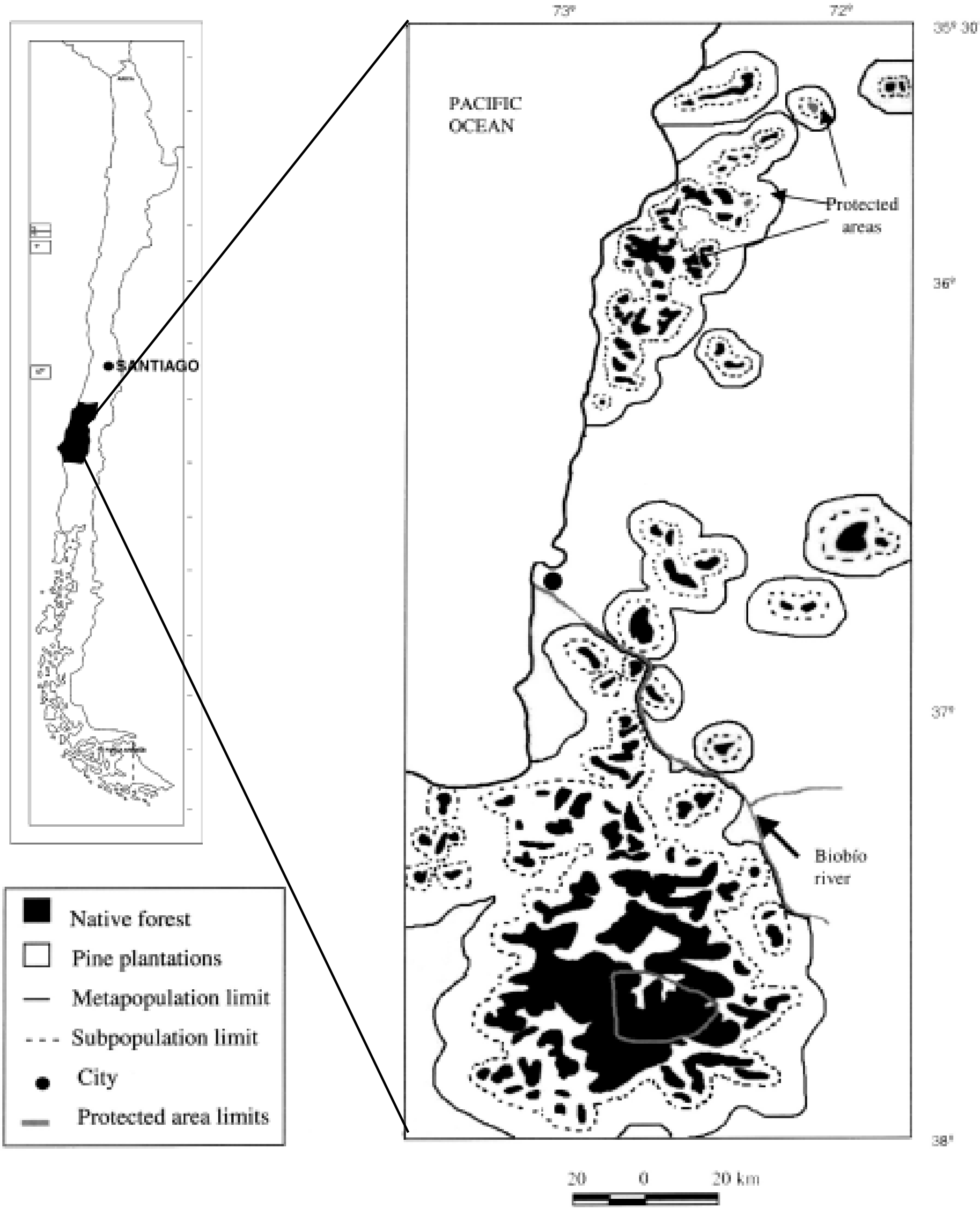

Fig. 2. Study area in central Chile. In black is native forest. In white are Pine plantations around native forest. Shaded lines depict subpopulations, and solid lines define *O. guigna* metapopulations. In gray lines see limit of protected areas: Los Ruiles Sector el Fin, Los Ruiles, Los Queules National Reserves and Nahuelbuta National Park in north-south order.

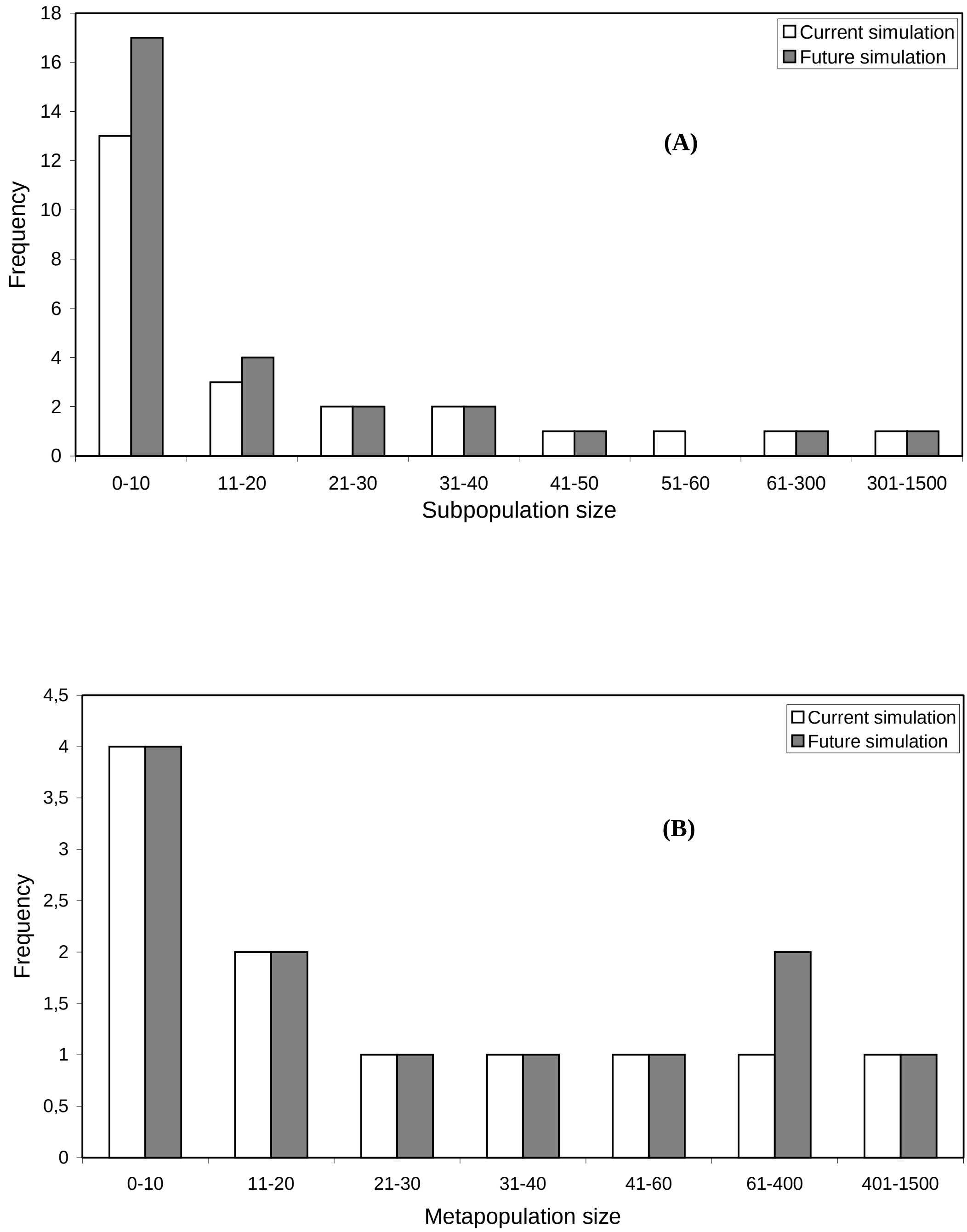

Fig. 3. **A)** Frequency distribution of *O. guigna* subpopulation sizes; **B)** Frequency distribution of *O. guigna* metapopulations sizes with 7.5 km of dispersal distance. Note that only one metapopulation (Nahuelbuta National Park) has more than 500 individuals and therefore should persist in a long time.

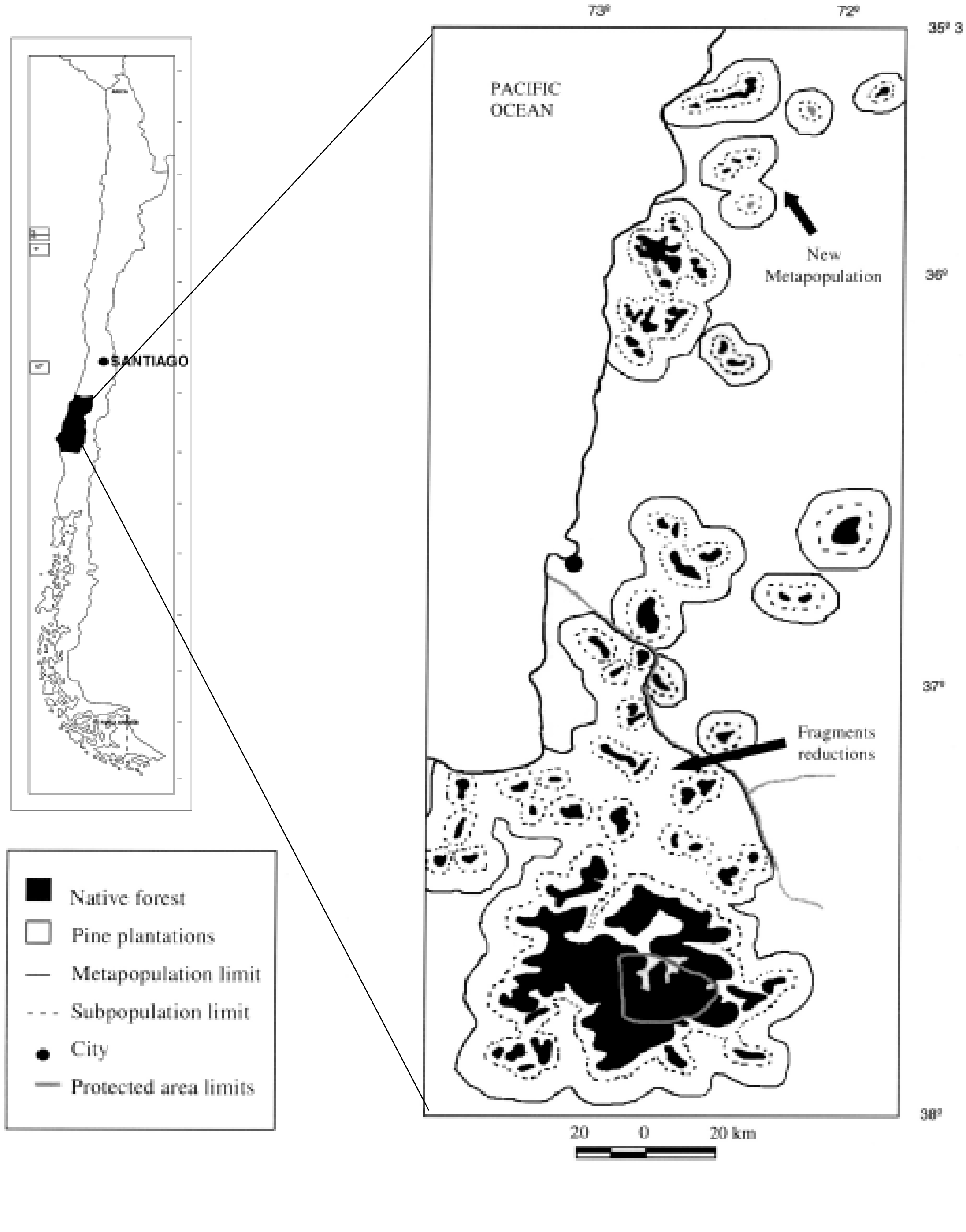

Fig. 4. Metapopulation delimitation with 7.5 km of dispersal distance and after extracting 30% of native forest fragments according to actual deforestation rate (20 years simulation). In black is native forest. Shaded lines depict subpopulations and solid lines define metapopulations of *O. guigna*. In gray lines see limit of protected areas.

Table 1

Current and future metapopulation classifications of *O. guigna* living in central coastal Chile range among 35 to 38º South, considering a maximal dispersal distance of 7.5 km.

Metapopulation type	Subpopulation type (Current/future)			Expected population size (Current/future)	Number of subpopulations (Current/future)
	Mainland	Midland	Island		
Mainland-island	1/1		8/17	1498/1173	9/18
Indeterminate		1/1	4/2	391/276	5/3
		1/1	2/2	63/63	3/3
Non-equilibrium			1/1	45/45	1/1
			1/	33/31	1/1
			1/1	16/16	1/1
			1/1	13/13	1/1
			1/1	7/7	1/1
			1/1	6/6	1/1
			1/1	4/4	1/1
			1/1	4/4	1/1
			0/1	0/12	0/2

improved but remained as indeterminate, and the central metapopulation conformed to an undeterminate metapopulation with more than 70 animals either, whether or not deforestation considered (**Fig. 5**). However, the distance between subpopulations was high with a dispersal distance of 11 km and in some cases bordering these limits and therefore far from potential recolonization.

DISCUSSION

The main conservation strategy operating in South American countries is to establish protected areas capable of maintaining biodiversity, viable populations of animals and ecological process (Simonetti, 1998). However, recent evidence suggests that a system of protected areas alone is not sufficient to preserve populations of wild carnivores that typically occur at low-densities (Simonetti and Mella, 1997; Woodroffe and Ginsberg, 1998; Kelly and Durant, 2000), and therefore it requires extensive areas of suitable non-protected habitat to remain viable.

In central Chile there are few protected areas, and most are smaller than 100 km^2; this is too small to provide adequate area to meet the maintenance requirements of viable populations of medium or larger sized mammals (>1 kg) (Armesto et al., 1998; Simonetti, 1999). On the basis of our theoretical model no protected areas in central coastal Chile would be able to sustain an *O. guigna* population in the long-term, due to their small size. Nahuelbuta National Park is capable of maintaining a viable population only in the short term, since this park could support only seventy animals in its 68 km^2 (see **Fig. 2**). Further north, Los Queules, Los Ruiles and El Sector el fin have a worse future, because of its small size (<1.5 km^2) would provide habitat only for two individuals.

However, these protected areas are not true islands, since they exist in a matrix of vegetation cover types (Fahrig and Merriam, 1985; Lovejoy et al., 1986; Stamps et al., 1987), outside of which there exist patches of similar habitat, which could contribute to the conservation of carnivores in a metapopulation scheme (Gotelli, 1991). Thus, according to these criteria, connectivity between protected areas is critical in the conservation of endangered species in a fragmented landscape to maintain viable metapopulation dynamics

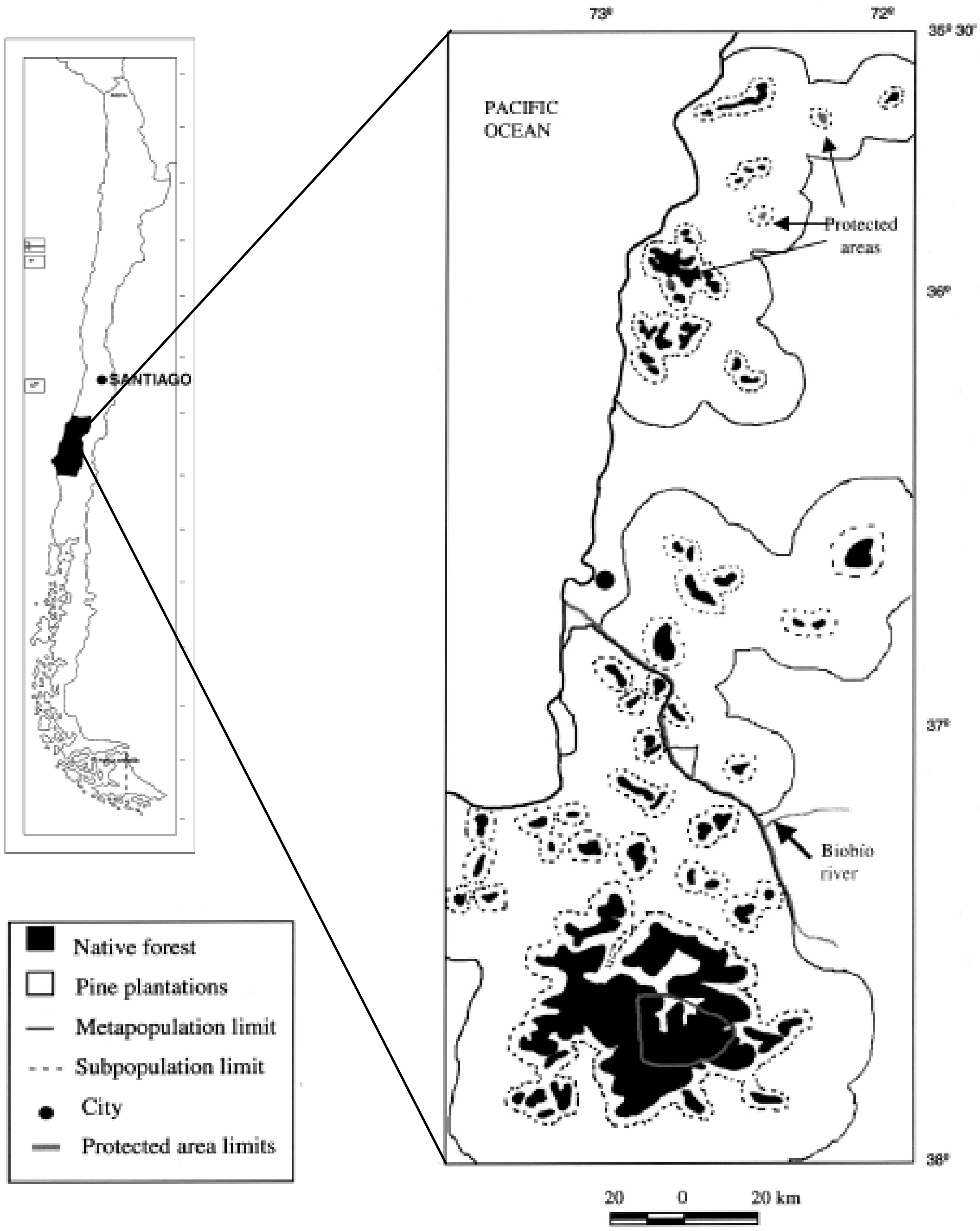

Fig. 5. Metapopulation delimitation with 11 km of dispersal (seven times the home range diameter and with a reduction of 30% native forest fragments according to actual deforestation rate, which correspond to 20 years of simulation). In black is native forest. Shaded lines depict subpopulations and solid lines define metapopulations of *O. guigna*. In gray lines see limit of protected areas.

(Taylor et al., 1993). Furthermore, it would serve to reduce the effective population size necessary to maintain a genetically viable population, allowing migration between fragments and increased probability of species survival (Samson et al., 1985). In fact, in Chiloé Island in Southern Chile, *O. guigna* use native forest to move throughout agricultural farms as corridors between forest patches of bigger size (Sunquist and Sanderson, 1998; Sanderson et al., 2002).

Because patches of suitable habitat for carnivores assume great importance, *O. guigna* survival according to this model would depend on the size and distance between native forest fragments as an index of habitat quality. In fact, Acosta and Simonetti (in press) found that this cat was associated to native forest patches of large size. Furthermore, in a field study on Los Queules National Reserve and plantations around it, Saavedra and Simonetti (in review) found rodent abundance to be higher in forest fragments and plantations than in continuous forest. Nevertheless, arboreal mammals as *Irenomys tarsalis* and *Dromiciops australis*, one of the main item prey in *O. guigna* diet, only were trapped in continuous forest (Dunstone et al., 2002b). Furthermore, birds are a secondary item preys, and Estades and Temple (1999) demonstrated in the same zone that richness of small birds is more abundant in native forest than pine plantations. Finally, vegetation structure and composition could be very important to explain *O. guigna* abundance, because arboreal rodents could be in higher densities in dense forests and would allow high *O. guigna* hunting success.

Thus, the largest areas of native forest will have a greater likelihood of maintaining viable populations. But, adjacent fragments would be necessary to maintain metapopulation dynamics with a source-sink structure acting, in some cases, as stepping-stones to assist genetic and demographic exchange between populations (Hanski et al., 1995; Hanski and Simberloff, 1997). Hence, to apply our metapopulation approach to the protected areas of Nahuelbuta and Los Queules, would require the presence of adjacent fragments; such fragments would be very important for the long-term maintenance of the Nahuelbuta metapopulation, and for Los Queules metapopulation, in the short-term.

Nevertheless, the increasing annual rate of deforestation outside of protected areas could increase the destruction of native forest fragments, which would reduce the potential for migration and genetic interchange between *O. guigna* populations, and hence threatens the persistence of this species in central coastal Chile (PAF, 1992).

The landowners of states surrounding protected areas are mainly private forestry companies. Therefore, the maintenance of *O. guigna* populations will require that all interested bodies, government (protected areas) and forestry companies work together, in the maintenance of corridors of native forest to allow dispersal of *O. guigna* and maintain its survival, reducing illegal hunting, human persecution and maintain the populations in the long term.

Because paucity of data on this secretive species we have used all available information at date, employing either empirical or theoretical information on movements capacity for cat species. However, it is necessary to continue obtaining more fieldwork data as dispersal distance, effect of competitors on movements capacity and prey offer, among other, to accurate this model. Between them, dispersal capacity through pine plantations appear as a relevant issue to elucidate in future studies. Finally, to improve this model we might incorporate more variables as illegal hunting and wildlife diseases transmitted by domestic animals.

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