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Abstract: 1. The ecology of the jaguarundi is poorly known, so I reviewed the literature for all original data and remarks on jaguarundi observations, ecology, and behaviour, to synthesize what is known about the species.

2. Jaguarundis occupy and use a range of habitats with dense undergrowth from northern Mexico to central Argentina, but may be most abundant in seasonal dry, Atlantic, gallery, and mixed grassland/agricultural forest landscapes.

3. Jaguarundis are principally predators of small (sigmodontine) rodents, although other mammals, birds, and squamate reptiles are taken regularly.

4. The vast majority of jaguarundi camera-trap records occurred during daylight hours (0600 h-1800 h); jaguaurndis are also predominantly terrestrial, although they appear to be capable tree climbers.

5. Home range sizes for jaguarundis vary greatly, but most are .25 km²; females' territories may be much smaller than or similar in size to those of males. Males may concentrate movements in one area before shifting to another and, as with other felids, intersexual overlap in habitat use appears to be common.

6. Interference competition may be important in influencing the distribution and ecology of jaguarundis, although their diurnal habits may somewhat mitigate its effect.

7. Conflict between humans and jaguarundis over small livestock may be widespread among rural human communities and is likely to be underreported. Despite this conflict, jaguarundis can persist in agriculturally modified landscapes and small forest fragments.

8. Additional research on local jaguarundi populations from more areas should be a priority to determine the true status of the species.



REVIEW

Ecology and status of the jaguarundi *Puma yagouaroundi*: a synthesis of existing knowledge

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ABSTRACT

1. The ecology of the jaguarundi is poorly known, so I reviewed the literature for all original data and remarks on jaguarundi observations, ecology, and behaviour, to synthesize what is known about the species.

2. Jaguarundis occupy and use a range of habitats with dense undergrowth from northern Mexico to central Argentina, but may be most abundant in seasonal dry, Atlantic, gallery, and mixed grassland/agricultural forest landscapes.

3. Jaguarundis are principally predators of small (sigmodontine) rodents, although other mammals, birds, and squamate reptiles are taken regularly.

4. The vast majority of jaguarundi camera-trap records occurred during daylight hours (0600 h–1800 h); jaguaurndis are also predominantly terrestrial, although they appear to be capable tree climbers.

5. Home range sizes for jaguarundis vary greatly, but most are $\leq 25 \text{ km}^2$; females' territories may be much smaller than or similar in size to those of males. Males may concentrate movements in one area before shifting to another and, as with other felids, intersexual overlap in habitat use appears to be common.

6. Interference competition may be important in influencing the distribution and ecology of jaguarundis, although their diurnal habits may somewhat mitigate its effect.

7. Conflict between humans and jaguarundis over small livestock may be widespread among rural human communities and is likely to be underreported. Despite this conflict, jaguarundis can persist in agriculturally modified landscapes and small forest fragments.

8. Additional research on local jaguarundi populations from more areas should be a priority to determine the true status of the species.

INTRODUCTION

The jaguarundi *Puma (Herpailurus) yagouaroundi* is a small, short-legged and elongated felid with a proportionally small head and low, rounded ears. Its rather atypical feline appearance has earned it such common names as otter cat and weasel cat (Guggisberg 1975). Three major pelage patterns exist: a chocolate brown to near black phenotype, which appears to be the most common; a greyishsilver phase; and a striking, although less common rust or reddish-brown colour (de Oliveira 1998a). Like its larger congeneric the puma *Puma concolor*, the jaguarundi is considered a generalist predator, one that occupies a broad spectrum of Neotropical habitats. Classified as a species of 'Least Concern' by the International Union for Conservation of Nature (Caso et al. 2008), the jaguarundi has unfortunately been the subject of little empirical research. To provide a thorough summary of what is known to date, I performed a comprehensive review of existing literature referencing aspects of jaguarundi ecology, as well as confirmed or purported observations, including peer-reviewed papers, theses, unpublished reports, anecdotal accounts, general mammal surveys, and regional faunal summaries. My goal here is to provide greater ecological context for the jaguarundi, and possibly to infer broader patterns with respect to the ecology, behaviour, and status of the species.

DISTRIBUTION AND HABITAT

The jaguarundi ranges from the USA-Mexico borderlands south through south-central Argentina (de Oliveira 1998a), making it second only to the puma among felids of the western hemisphere in its overall latitudinal expanse (Fig. 1). Parts of the jaguarundi's distribution, however, are incompletely understood, possibly because of a lack of research interest or funding to study the species, and its current 'Least Concern' status (Caso et al. 2008). Survey information from the northern limit of the jaguarundi's range, for example, including broad parts of southern Texas, USA, and northern Mexico, is still lacking; this makes purported observations difficult to confirm and a matter of continuing debate. In extreme south Texas and northern Tamaulipas, Mexico, thornscrub habitats have historically been considered the northernmost limit of the species' geographical range (Goodwyn 1970, Tewes & Everett 1986, Caso 1994). Although recent unconfirmed sightings exist from the vicinity of Laguna Atascosa Wildlife Refuge, Texas, the last confirmed jaguarundi in the USA appears to have been a road-killed individual near Brownsville, Texas in April 1986 (Grassman & Tewes 2004). Based on reliable observations (i.e. those for which the observer was consid-



Fig. 1. Currently accepted geographical range in south and central America, shown in dark grey, for the jaguarundi *Puma (Herpailurus) yagouaroundi* (modified with permission from Sunquist & <u>Sunquist</u> <u>2002);</u> approximate areas of ambiguity at the northern end of the jaguarundi's range are shown as '?'.

ered knowledgeable and the context was considered credible) collected between 1970 and 1982, Everett (1983) and Tewes and Everett (1986) suggested that the jaguarundi may have recently ranged north and west from south Texas across the southern Edwards Plateau, and north along the entire coastal plain of east Texas. Its current existence in this region, its occurrence in the Pecos region of Texas and northern Coahuila, Mexico, and whether or not it occurs or has occurred in parts of southern Arizona, USA and Sonora, Mexico, remains unresolved (Little 1938, Brown & Lopez-Gonzalez 1999, Grigione et al. 2007, 2009, Giordano et al. 2011), and physical evidence is lacking (Fig. 1). Despite the ambiguity, new, confirmed jaguarundi records from additional areas of Mexico, including the first from Mexico's central highlands (1324 m; Charre-Medellin et al. 2012), have occurred recently.

The jaguarundi occupies a diversity of habitats throughout its range (de Oliveira 1998a), including pine-oak forest associations in central Mexico (Monroy-Vilchis et al. 2011, Charre-Medellin et al. 2012). It is probably best known, however, from more tropical and subtropical habitats, particularly areas with dense undergrowth or open areas with thick bushes and grasses (de Oliveira 1998a). Rengger (1830) claimed that the jaguarundi was perfectly adapted to the dense thickets, scrub, and tangled undergrowth where it was frequently encountered, and asserted that these habitats, as well as hollow trees and ditches overgrown with scrub, afforded suitable den sites for the species. Snow (in Davis 1974) claimed that jaguarundis in extreme southern Texas denned under fallen trees overgrown with thick grass and shrubs, or in dense thickets.

Based on 95% fixed kernel home range locations recorded in coastal Tamaulipan thornscrub, 18 jaguarundis used mature subtropical deciduous forest (48%) and Guinea grass mixed agricultural habitats (45%) similarly, but appeared to prefer the forest based on its availability (Caso 2013). Males used forest habitats (53%) more than females (43%) and avoided Guinea grass pastureland, whereas females used the latter habitat in proportion to its availability. Both male and female jaguarundis preferred forest habitat based on its availability. Red colour phase jaguarundis (n = 7) preferred forest habitat (54%) more than grey phase jaguarundis (n = 9; 45%) and avoided other habitats; grey phase jaguarundis also preferred Guinea grass habitats (47%) and used native Gulf cordgrass in proportion to its availability (Caso 2013).

Along the central pacific coast of Mexico, interviews suggested that the jaguarundi may favour habitats such as Sinaloan thornscrub, as well as dry subtropical deciduous forest with thick undergrowth (e.g. Guerreran dry deciduous forest type; Brown & Lopez-Gonzalez 1999). Monterrubio-Rico et al. (2012) recorded several jaguarundi occurrences from Michoacán, Mexico and suggested they were contiguously distributed along the southern Sierra Madre. Edward Nelson (in Guggisberg 1975) reported an anecdotal account by locals that jaguarundis showed a preference for riparian areas in coastal Guerrero, Mexico. Several records from Mexico are also associated with riparian areas, including a den of jaguarundi kittens on a forested river bank (Sanchez et al. 2002). Approximately 25% of jaguarundi records (n = 58) obtained via interviews in San Luis Potosi, Mexico, originated from high grassland areas, followed by agricultural areas (21%) and tropical forests (19%; Quibrera 2011). Although she incorporated records of varying credibility from interviews, including second-hand observations, Quibrera (2011) concluded that surrounding vegetation and ambush cover appeared to be the most significant habitat variable influencing jaguarundi presence, regardless of habitat type. In the Selva Lacandona of Chiapas, Mexico, the jaguarundi has also been recorded from wetter tropical forests (Garcia-Alaniz et al. 2010).

Presumably the jaguarundi still ranges across suitable habitat in Central America, and in the Yucatan Peninsula, its presence is well known. Rabinowitz (1984) spotted jaguarundis frequently in the Cockscomb Basin of Belize while conducting research on jaguars Panthera onca. Based on a total of 106 telemetry location points over a 14-month period, Konecny (1989) found that three radio-collared jaguarundis in Cockscomb were located most frequently in disturbed habitats, such as abandoned agricultural fields and secondary growth near water; the latter habitat was where the three animals were originally captured. The same data indicated a strong preference for riparian habitats, and one den site, an abandoned paca Cuniculus paca den, was apparently located on the bank of a small stream (Konecny 1989). In Costa Rica, where jaguarundis are rare and classified as 'in danger of extinction', they reportedly occur throughout suitable habitat along both the Atlantic and Pacific Coasts at elevations up to 2000 m (Anonymous 2008), including in the disturbed, secondary forests of Guanacaste Conservation Area (Harrison 1997), the Reserva Natural Absoluta Cabo Blanco on the Nicoya Peninsula (Timm et al. 2009), and other heavily impacted dry forest landscapes.

In South America, jaguarundis are widely distributed across the full range of relatively low elevation biomes (<2000 m; record elevation 3200 m in Columbia; Cuervo et al. 1986), but appear to be absent west of the Andes from northern Peru on southward to their range limit (Fig. 1). In Venezuela, jaguarundis are reportedly the most common and widely distributed felid in the lowlands (up to 900 m elevation) north of the Orinoco River (Mondolfi 1986, Bisbal 1987), while few records originated from south of the river. Tropical dry forests apparently yielded the highest capture rates of the species, although deciduous gallery forest, adjoining open palm savanna and brushland, and riparian areas were all also associated with jaguarundi records (Mondolfi 1986, Bisbal 1989). East and west of the Ecuadorian Andes, jaguarundis occur throughout the tropical zones (Rodriguez et al. 1989), although specific occurrence data are lacking there as many places. In Peru, the jaguarundi occurs throughout the high forests of San Martin, Huanuco, Pasco, and Puno regions, the low forests of Loreto and Madre de Dios regions, protected areas such as Yanachaga-Chemillen and Tingo Maria National Parks, and Pacaya-Samiria Nature Reserve (Pulido 1991), and in the wet forests and dry forest floodplain of Manu Biosphere Reserve and its buffer zone (Salvador et al. 2011). Jaguarundis also inhabit every major ecoregion in Brazil, including Pantanal, Cerrado, Caatinga, tropical forest of the Amazon, Atlantic forest, gallery forests, and disturbed or secondary vegetation of varying habitat types (de Oliveira & Cassaro 1997, de Oliveira 1998a, Nakano-Oliveira 2002, Trovati 2004, de Oliveira et al. 2010). In the eastern Amazon, jaguarundis were present in three out of four small clustered tropical forest fragments surveyed, and one was observed in a 2 km² tract of primary forest surrounded by 6 km² of disturbed forest (Stone et al. 2009). In Sao Paulo, Brazil's most populous and developed region, jaguarundis have been observed crossing roads in secondary Atlantic Forest at 750-900 m elevation, and also moving in *restinga* vegetation (i.e. thick, coastal forest vegetation occupying sandy soils or 'spits' along water; Guix 1997). They also occurr in fragmented cerrado (Lyra-Jorge et al. 2007), where gallery forests might play an important role in maintaining populations of jaguarundis and their prey (Johnson et al. 1999), as well as in the Atlantic Forest reserves of Rio Grande do Sul along the Brazil-Argentina border (Kasper et al. 2007, Melo et al. 2012).

Michalski et al. (2006) found that a radio-collared female jaguarundi in Brazil selected secondary forest over other adjacent habitats, whereas a male appeared to use all habitats (e.g. semi-deciduous Atlantic forest, grassland savanna, *Eucalyptus* plantation) in proportion to their availability; however, both animals were monitored only sparsely (every 18–34 days) over a 6- to 12-month period. A radio-collared female jaguarundi from Emas National Park used scrub savannah slightly more than in proportion to its availability while using a small area of gallery forest less; grassland savanna and agricultural lands were used in proportions similar to their availability (de Oliveira et al. 2010).

In Paraguay, I have observed jaguarundis in similarly degraded habitats (e.g. *Eucalyptus* plantation, mixed agricultural grassland encroaching in the Upper Parana Atlantic Forest ecoregion), primary Atlantic Forest, and most frequently, during the dry season in the Gran Chaco; all were not far from dense, dry forest undergrowth, although not necessarily close to riparian areas. In Argentina, <u>Pereira</u> et al. (2011) recorded a jaguarundi from the central

 Table 1. Summary of the relative frequency of all animal prey

 occurrences by the jaguarundi Puma yagouaroundi as reported in 14

 published accounts in the literature

	Number (%)		
Prey species	Scats	Stomach	Total*
Mammals	159	23	205 (58.6)
Rodents	130	20	152 (43.4)
Marsupials	29	0	29 (8.3)
Other	6	3	9 (2.6)
Unidentified	15	0	15 (4.3)
Birds†	26	11	37 (10.6)
Passeriformes	2	6	8 (2.3)
Non-Passeriformes	2	3	5 (1.4)
Unidentified	22	2	24 (6.9)
Reptiles	20	12	32 (9.1)
Lizards	5	12	17 (4.9)
Snakes	12	0	12 (3.4)
Unidentified	3	0	3 (0.9)
Invertebrates (arthropods)	75	0	75 (21.4)
Fish	1	0	1 (0.3)
Total	302	46	350

*Includes two kills purportedly made by jaguarundis and not included in the prior two columns.

+Bird records do not include domestic animals; no more than one 'arthropod' occurrence is considered per scat.

Argentine Monte. Lucherini et al. (2004) suggested that Atlantic Forest, Aracucaria Tropical Forest, Andes Tropical Forest, Chaco, and Argentine Monte were better habitat for jaguarundis than Pampas and Puna Habitat Units, and all were better suited than Patagonian steppe and southern Andean Patagonian forests. Rigorous habitat association studies however are lacking from these areas.

DIET

Like other small Neotropical felids, the jaguarundi appears to be a generalist predator of small vertebrates (de Oliveira & Cassaro 1997, de Oliveira 1998a,b). The little that is known is based on a few studies relying on purported jaguarundi scats and some opportunistic examinations of stomach contents. Mammals played the most important role in the diet of jaguarundis, constituting nearly 60% of prey items from 14 published accounts (Table 1). Tofoli et al. (2009) reported that small mammals comprised approximately 43% of all prey occurrences in scat (n = 74) and regurgitate samples (n = 26) from Atlantic Forest and agricultural habitat in southeastern Brazil.

Overall, sigmodontine rats (e.g. Sigmodon, Oryzomys, Zygodontomys) accounted for nearly half the mammals taken by jaguarundis throughout their range (Fig. 2) and were taken with greater frequency than other prey in Venezuela, the coastal Atlantic forests of Brazil, seasonal dry forests of Mexico's Pacific coast, and the Cockscomb Basin of Belize (Bisbal 1986, Mondolfi 1986, Konecny 1989, Facure & Giaretta 1996, Guerrero et al. 2002). Bisbal (1986) recovered the remains of eight juvenile Sigmodon from the stomach of one jaguarundi, and noted that Eisenberg et al. (1979) considered sigmodontine rats (e.g. Zygodontomys) to be among the most abundant mammals in the Venezuelan Llanos. Mondolfi (1986) also recorded sigmodontine rats (e.g. Sigmomys, Sigmodon, Oryzomys) as jaguarundi prey in Venezuela, noting that the stomach of a road-killed juvenile female contained four. In mixed natural grassland and pine forest of southern Brazil (Parana), sigmodontine rats comprised approximately 54% of all prey items recorded in jaguarundi scats (n = 51); unidentified cricetid rodents

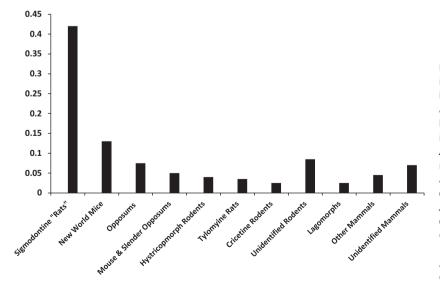


Fig. 2. Relative proportion of mammalian taxa in the diet of jaguarundis, reported in 14 published accounts as occurring in scats and stomachs. 'Sigmodontine rats' are defined here as larger Sigmodontine rodents (Cricetidae) including Sigmomys, Sigmodon, Oryzomys, Zygodontomys, etc. The category 'New World mice' is a polyphyletic grouping based on size, and includes Peromyscus and Reithrodontomys (Neotominae; Cricetidae), Thaptomys and Akodon ('sigmodontine mice'), and Liomys (Heteromyidae). 'Cricetine rodents' (Cricetinae; Cricetidae) are hamsters and their relatives. 'Opposums' include Didelphis, Caluromys, Philander, etc., while 'Mouse & Slender Opposums' include Marmosa, Marmosops, etc.

comprised another 22% of prey (Silva-Pereira et al. 2010). 'New World mice' (e.g. Peromyscus, Liomys, Reithrodontomys) constituted the second most important mammal group, but occurred much less frequently (13% of mammals, Fig. 2; Konecny 1989, Guerrero et al. 2002, Tofoli et al. 2009, Rocha-Mendes et al. 2010). Not all rodents were identified to species in some studies. Tofoli et al. (2009) could not identify to species the rodents in 15% of jaguarundi samples (n = 26), and Guerrero et al. (2002) failed to identify approximately 7% of all prev occurrences (n = 112) in scats. Small mouse opossums, short-tailed opossums, slender opossums that forage on or close to the ground (e.g. Monodelphis, Gracilinanus, Marmosops, Marmosa), and some larger opossums (e.g. Caluromys philander, Philander frenatus), were recorded as prev in the Atlantic Forest ecoregion (Tofoli et al. 2009, Rocha-Mendes et al. 2010, Bianchi et al. 2011).

Hystricomorph rodents (e.g. cavies, spiny rats, agoutis) are also part of the jaguarundi's diet (e.g. Olmos 1993, Tofoli et al. 2009), although they comprised only approximately 4% of total prey occurrences I could find (Fig. 2). A Brazilian guinea pig Cavia aperea was recovered from the stomach of a female jaguarundi in southeastern Brazil (Manzani & Monteiro Filho 1996), while the remains of a vellow-toothed cavy Galea spixi were recorded from a purported jaguarundi scat in the Brazilian caatinga (Olmos 1993). Olmos (1993) described the still articulated skeletal remains of a rock cavy Kerodon rupestris in Serra de Capivara National Park with the skin pulled back around the head and viscera removed; he believed this to have been killed and eaten by a jaguarundi, although he offered no evidence as to why. On one occasion, I encountered the remains of a giant Chaco tucu-tucu Ctenomys conoveri in the Paraguayan Chaco which appeared to have been killed and eaten in the same manner (i.e. skeleton still articulated, with the skin pulled back around the head and viscera removed). Although I found it relatively fresh in late afternoon and along a road where I frequently observed jaguarundis, it was impossible for me to exclude the possibility that another small felid (e.g. an ocelot Leopardus pardalis) killed this animal.

Larger mammals are also taken by jaguarundis, but rarely so (Fig. 2). The common opossum *Didelphis marsupialis* occurred in 13% of all jaguarundi scats (n = 46) Konecny (1989) collected in the Cockscomb Basin of Belize, the largest prey animal he recorded. Facure and Giaretta (1996) documented two occurrences of Brazilian cottontails *Sylvilagus brasiliensis* in six scats from the Atlantic Forest, while in Venezuela, Mondolfi (1986) and Bisbal (1986) recorded cottontails *Sylvilagus floridanus* in two of 13 stomachs, and in one stomach, respectively. A jaguarundi from the same region was also observed chasing and attacking a long-nosed armadillo *Dasypus* sabanicola, and this prey species also occurred among the stomach contents of a dead animal (Mondolfi 1986). The naked-tailed armadillo Cabassous tatouay was a rare prey item in the Brazilian Atlantic Forest, as was a single record of brocket deer Mazama sp.; Tofoli et al. 2009), which the authors assert was probably scavenged from a puma in the area where and when jaguarundi scats were collected. Rengger (1830) remarked casually that jaguarundis may take fawns but references no specific observation. Wang (2002) reported both paca and three-toed sloth Bradypus variegatus as occurring in the only three purported jaguarundi scats she collected from the Atlantic Forest; along with the brocket deer, these are among the largest species recorded as jaguarundi prey. Another study from the same ecoregion reported brocket deer Mazama nana and paca as occurring in jaguarundi scats (Rocha-Mendes et al. 2010). Whereas these could represent instances of scavenged prey, or young animals that were taken opportunistically, it is possible that scats from these or any study discussed above were misidentified; conversely, such prey may represent the upper size limit for jaguarundis.

It is clear that non-mammalian prey is important in the jaguarundi's diet. Birds occurred with the next greatest frequency after mammals (11%; Table 1), although only slightly more than reptiles (9%) overall. Dalquest (1963), Snow (in Davis 1974) and Rengger (1830) were of the opinion that the jaguarundi was a cursorial bird specialist; most of their accounts however were probably biased toward conflict-related contexts. In Venezuela, one author recorded birds (n = 7), mostly unidentified passeriforms, more frequently than mammals (n = 4) among the stomach contents of 10 jaguarundis (Bisbal 1986), while another documented unidentified passeriforms in 7 of 13 stomachs from roadkills (Mondolfi 1986). The remains of a tinamou (Tinamidae) and a pigeon or dove (Columbidae), two ground-foraging birds, were recovered from the stomach of a male jaguarundi from the Atlantic Forest (Manzani & Monteiro Filho 1996); similarly, Zuercher (2001) recorded a tinamou from a confirmed jaguarundi scat collected in the Atlantic Forest of Paraguay. In other studies, the remains of a small number of birds in jaguarundi scats either could not or were not resolved to species (e.g. Olmos 1993, Facure & Giaretta 1996). For example, 'small birds' were reported from nearly 22% of all scats (n = 46) from the Cockscomb Basin (Konecny 1989). Similarly, Guerrero et al. (2002) reported approximately 7% of prey only as 'birds'. Tofoli et al. (2009) did not specifically identify the birds occurring in 16% of all jaguarundi samples (n = 26); they coarsely identified birds (as 'passerine', 'non-passerine', etc.) in another 6% of their samples.

Teiid, iguanid, and tropidurid lizards, and a few snakes (e.g. colubrid, viperine), are among the common reptilian prey of jaguarundis from Belize, Venezuela, and Brazil, (Bisbal 1986, Olmos 1993, Facure & Giaretta 1996, Manzani & Monteiro Filho 1996, Guerrero et al. 2002, Tofoli et al. 2009, Bianchi et al. 2011; Table 1). <u>McCarthy (1992)</u> witnessed a jaguarundi stalking an adult iguana *Iguana iguana* on the banks of the Temash River in Belize, while Manzani and Monteiro Filho (1996) reported on opportunistic jaguarundis preying upon characid fish *Astyanax bimaculatus* trapped in drying puddles. A fish also appears to have been prey in the dry forests of Mexico, and insects constituted 24% of all prey remains by occurrence in scats collected from the same site (Guerrero et al. 2002).

Invertebrates (primarily arthropods) were taken at several sites and constituted 21% of prey occurrences in the literature. In the Cockscomb Basin, the remains of arthropods were the single most frequently occurring prey category (>70%) in jaguarundi scats (n = 46), more than twice the occurrences in margay *Leopardus weidii* scats (n = 27) from the same region, and seven times as many as in ocelot scats (n = 49; Konecny 1989). Invertebrates occurred in 20% of jaguarundi samples collected from a disturbed Atlantic Forest landscape in southeastern Brazil (Tofoli et al. 2009), and Olmos (1993) recorded a *Scolopendra* centipede as prey in the Brazilian caatinga. Overall, although not constituting the biomass of other prey items, arthropods and other invertebrates may help sustain jaguarundis between capture and consumption of larger prey.

ACTIVITY AND ARBOREAL BEHAVIOUR

Evidentiary support for the jaguarundi's predominantly diurnal behaviour can be found in both camera-trapping (Fig. 3) and telemetry activities from throughout its range. Eight camera-trap records of jaguarundis from the Dry and Transitional Paraguayan Chaco occurred during daylight hours (A. J. Giordano, unpublished data) and no photos of jaguarundis were recorded at night from these locations. In the dry Chaco-Chiquitano forests of Bolivia, Maffei et al. (2002) logged 14 camera-trap records of jaguarundis, all of which occurred between 0400 h and 2000 h. In the same region, Maffei et al. (2007) recorded nearly 40 camera-trap records of jaguarundis, all between 0500 h and 1800 h, and in Brazil, Kasper et al. (2007) recorded 20 jaguarundi photos, none of which was taken between 2000 h and 0600 h. In the Upper Parana Atlantic Forest, the jaguarundi appears to be exclusively diurnal: all camera-trap records of the species (n = 45) occurred between 0530 h and 1830 h (Di Bitetti et al. 2010). Of the seven total photographic records of jaguarundis recorded in Michoacán by Monterrubio-Rico et al. (2012), all occurred during daylight hours.

The combined movements of one female and two male jaguarundis monitored via radiotelemetry during a 10- to 14-month study in the Cockscomb Basin suggested that jaguarundis could be active all hours (Konecny 1989), although not equally so. Daily patterns exhibited a pronounced increase around the pre-dawn hours (0400 h), peaking during late morning (1100 h) and decreasing steadily through the early afternoon (1300 h), with most activity ceasing around sunset (1800 h). On a few occasions during a given night, Konecny (1989) recorded an animal being active for longer than two consecutive hours; there was slightly more activity on moonlit as opposed to dark nights. A telemetry study of 13 male and 8 female jaguarundis in the Tamaulipan thornscrub of northern Mexico showed that jaguarundis were active throughout the day, with peak diel periods occurring between 1100 h and 1400 h (Caso 2013). Like Konecny (1989), Caso (2013)

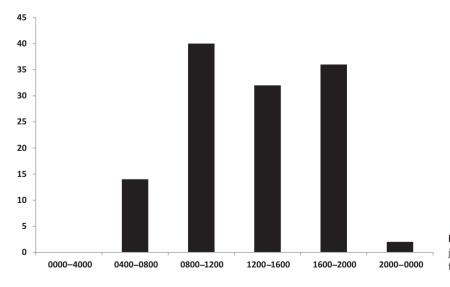


Fig. 3. Number of camera-trap records (y) of jaguarundis for discrete diel periods in h (x) from 10 published and unpublished accounts.

found that although jaguarundis could be active all hours, nocturnal activity was uncommon, and diurnal movements accounted for >85% of all activity.

Most eyewitness accounts provide strong evidence that the jaguarundi is almost exclusively diurnal and terrestrial, though it is important to consider than this is when observers may have been most active. Mondolfi (1986) communicated several observations of jaguarundis made by colleagues working in Venezuela spanning from midmorning (0810 h, 0910 h, 1015 h) to late afternoon and early evening (1600 h, 1700 h, 1800 h, 1845 h, 1915 h), with only one in the middle of the night (0053 h). Of 11 observations of jaguarundis in the Cockscomb Basin made by Konecny (1989), all but one occurred during the day. Two observations made by Guix (1997) in the Atlantic Forest region occurred during the day, while on 10 different occasions (2008-2011) when I observed jaguarundis in the Dry Chaco and Atlantic Forest regions of Paraguay, all occurred during daylight hours (0700-1630 h). In addition, during his telemetry study, Caso (2013) made 21 first-hand observations of jaguarundis during the daytime.

McCarthy (1992) described several encounters with jaguarundis in Belize and Guatemala, all but one of which occurred during daylight and were terrestrial encounters; another more prolonged encounter spanned a night and early morning, during which two jaguarundis were active among tree branches in the mid-canopy. F. B. Armstrong, as communicated by Bailey (1905), appears to have also witnessed jaguarundis in trees, and claims to have shot one out of a tree at night. Another account from Chiapas, Mexico suggests that jaguarundis are skilful climbers and can jump up, from, and among trees of some distance and height with relative ease, and characterizes them as only occasionally nocturnal (del Toro 1977). Rengger's (1830) early accounts from Paraguay, while suggesting that jaguarundis were primarily terrestrial and diurnal, also describe them as skillful and agile in the trees, to which they often took to when pursued by hounds.

MOVEMENTS AND HOME RANGES

Although jaguarundis have been the subject of comparatively fewer research studies than other Neotropical felids (e.g. jaguars, pumas, ocelots), some information on home ranges does exist. Konecny (1989) provided good detail regarding one female and two male jaguarundis monitored in the Cockscomb Basin. The overall mean hourly movements for the three cats was 0.25 km, with a maximum of 2.25 km, and diurnal means (0.28 km) significantly greater than nocturnal means (0.09 km). Mean total daily distance travelled in five 24-hour periods of monitoring was 6.6 km, and the home ranges of the males (~88 and 100 km²) were four- to fivefold larger than that of the female (~20 km²). There was also little predictable 'cyclicity' to their movements. Sampling was restricted to these three individuals, and speculation remains as to the explanation for these very large male home ranges. It is possible that males were avoiding intraspecific competition or predation, or monitoring the reproductive state of overlapping females (Konecny 1989). Regardless, the home ranges of these jaguarundis were actually several times larger than those of the much larger sympatric jaguars as reported by Rabinowitz & Nottingham (1986). In an agricultural landscape with subtropical forest fragments in southern Brazil, the average home range of three male jaguarundis was much smaller (23.4 km²; de Oliveira et al. 2010), but still relatively large for a small felid.

Other studies indicate that the home ranges of jaguarundis are more comparable to the findings of de Oliveira et al. (2010), at least in some geographical regions or habitats. In Iguaçu National Park, the home range of a male jaguarundi (17.6 km²) was several times larger than that of a female (6.8 km²; Crawshaw 1995), while in the Brazilian cerrado, a male's home range (25.3 km²) was only somewhat larger than a female's (18 km²; Trovati 2004). In a 50-km² disturbed forest and grassland mosaic that included Ipanema National Forest (Sao Paulo, Brazil), the home range of a male jaguarundi (20.47 km²) was substantially larger than that of a female (1.88 km²), although the latter was monitored for half as long (6 months) as the former (12 months; Michalski et al. 2006). This female appeared to restrict her movements entirely to secondary forest, despite the fact that it represented only 45% of the habitat available to her. Michalski et al. (2006) may also have underestimated the home ranges of the jaguarundis due to large intervals (18-34 days) between consecutive locations recorded. Consistent with Konecny (1989), both Crawshaw (1995) and Michalski et al. (2006) found that male jaguarundis changed their movements, using smaller, restricted portions of their home range before shifting or 'disappearing' to another portion.

In northern Tamaulipas, Mexico, the mean 95% kernel and minimum convex polygon home ranges of 10 male jaguarundis $(16.5 \pm 5.05 \text{ km}^2 \text{ and } 10.73 \pm 4.74 \text{ km}^2, \text{ respec$ $tively})$ was not significantly larger than that of eight females $(12.09 \pm 5.16 \text{ km}^2 \text{ and } 8.59 \pm 2.65 \text{ km}^2, \text{ respectively})$ using either estimator, and both intra- and inter-sexual home range overlap was extensive (Caso 2013). Mean daily movements for the same 10 male jaguarundis $(1.46 \pm 0.87 \text{ km})$ were greater than for the eight females $(0.88 \text{ km} \pm 0.66)$; males also travelled significantly further $(2.13 \pm 0.38 \text{ km})$ than females $(0.52 \text{ km} \pm 0.28)$ during 24-hour tracking periods, as well as moving significantly more per hour on average $(387 \pm 209.8 \text{ m vs. } 180.67 \pm 140.5 \text{ m};$ Caso 2013).

ECOLOGICAL AND SOCIAL INTERACTIONS

Jaguarundis are frequently sympatric with three larger Neotropical felids (jaguars, pumas, ocelots) and one to two similar-sized Neotropical felids (Leopardus sp.), and some ecological partitioning has been observed among these species. In Venezuela, ocelots exhibited a greater richness $(n_{\min} = 10)$ of prey species than jaguarundis $(n_{\min} = 3)$ overall (Bisbal 1986). Mammals also constituted a greater percentage of the dietary volume of ocelots (88%) than of jaguarundis (46%), whereas jaguarundis took more birds and reptiles. In the Cockscomb Basin, the activity patterns of both the jaguarundi and the tayra Eira barbara were similarly diurnal and together very different from those of ocelots and margays; margays were strongly nocturnal and became more active around the same time jaguarundis were becoming less active (1300-1600 h; Konecny 1989). Konecny (1989) further reported that the diversity of prey species taken by jaguarundi and tayra appeared to be highly correlated (R = 0.694, P = 0.001), although the proportional occurrence of prey items in the diet of each predator overlapped by approximately 40% (Konecny 1989). The author also recorded arthropods in jaguarundi scats (n = 46) sevenfold more frequently than in ocelot scats (n = 49), more than twice as frequently as in margay scats (n = 27), and 20% more than in tayra scats (n = 31). In addition, jaguarundis preyed upon more birds and rodents overall than ocelots, the latter of which consumed more opossums in Belize (Konecny 1989); in this respect, the jaguarundi's diet was more similar to that of the margay.

Sanchez-Cordero et al. (2008) concluded that among all pairwise comparisons of potentially sympatric felids native to Mexico, the highest geographical overlap was between jaguarundis and margays (98%), followed by pumas and bobcats Lynx rufus (97%). Kiltie (1984) concluded that the craniomandibular characteristics of both jaguarundis and margays were functionally similar, suggesting that they are ecologically equivalent predators in their respective niches (the jaguarundi is primarily terrestrial and diurnal, the margay is at least partly arboreal and strongly nocturnal). That this might facilitate coexistence is at least partly supported by the findings of Konecny (1989), as well as by camera-trap research from northeastern Argentina. In the Green Corridor of Misiones, Di Bitetti et al. (2010) found no overlap in activity patterns between jaguarundis and margays, the only pairwise comparison of felids to exhibit this exclusivity; peaks in their activity patterns differed by 11- to 12-hour intervals. In the Atlantic forests of southern Brazil, Bianchi et al. (2011) recorded birds most frequently (55%) in a small number of jaguarundi scats (n = 9); in comparison, small mammals (77%) appeared to dominate margay scats (n = 30) from the same region, followed by birds (53%). From the same region, limited scat analysis

(n = 14) by Rocha-Mendes et al. (2010) suggested that jaguarundis had the broadest dietary niche in a carnivore community that included ocelots and margays. Guerrero et al. (2002) concluded that the niche breadth of jaguarundis was much smaller than that of sympatric arctoid carnivores (e.g. coyotes Canis latrans, grey foxes Urocyon cinereoargenteus, raccoons Procyon lotor) in Mexico, noting that overlap was smallest with raccoons (20%) and highest with covotes (>50%). In the Devonian Scarp landscape of southern Brazil, sigmodontine rodents comprised a greater proportion of prev occurrences in ocelot scats (~67%; n = 21) than in jaguarundi scats (~54%; n = 51), and ocelots took more larger mammals (>1000 g; Silva-Pereira et al. 2010). Jaguarundis also appeared to take more birds than ocelots, which along with the relatively high proportion of rodents, put them in greater competition with the oncilla Leopardus tigrinus, the niche of which overlapped considerably with the jaguarundi (Pianka's Overlap Index = 0.95; Silva-Pereira et al. 2010).

Larger and similar-sized mesocarnivores may play a role in influencing the occurrence, density, and/or distribution of jaguarundis, and jaguarundis might benefit from the absence of such species. The existence of an 'ocelot effect' (de Oliveira et al. 2010), for example, has been proposed for small felids (e.g. jaguarundis, oncillas). From 2001-2004, Maffei et al. (2007) recorded more than 20-fold more camera-trap photos of ocelots than of jaguarundi and of Geoffroy's cat Leopardus geoffroyi in the Bolivian Chaco, both of which were also recorded less than one-third as frequently as pumas and jaguars. For 196 camera-trap stations at six sites in the Upper Parana Atlantic Forest where each station was active for 21 days, records for jaguarundis (n = 43) were 5% of the records of ocelots, 11% those of pumas, 35% those of oncillas, and 56% those of jaguars (Di Bitetti et al. 2010); only margays (n = 35) were recorded less frequently, possibly due to their more arboreal nature (Guggisberg 1975, de Oliveira 1998b). Despite the relatively low number of records, the authors concluded that jaguarundi occupancy or abundance was not negatively impacted by the presence of ocelots, probably because jaguarundis were diurnal. In the absence of ocelots in central Argentina, Pereira et al. (2011) recorded a low jaguarundi detection rate of only 0.2/100 trap days; in contrast, detection rates for Geoffroy's cats for the same study area were at least eightfold higher, depending on the time period. Caso (2013) noted that differences in habitat use and activity patterns probably facilitated the coexistence of ocelots and jaguarundis in the same landscape in northeastern Mexico. He reported that while jaguarundis used open grassland areas more and woodland communities less than ocelots and were the more diurnal species, telemetry data indicated that both species exhibited local avoidance of one another when they were tracked in the same area.

Competitive interactions with bobcats may contribute to limiting the northern distribution of jaguarundis. While Sanchez-Cordero et al. (2008) suggested that Neotropical cat communities are a key limiting factor in the southernmost distribution of bobcats, Horne et al. (2009) concluded that bobcats selected for more open areas (i.e. areas with <75% canopy cover) than ocelots, which suggests they may prefer the same types of habitats as jaguarundis. Although bobcats are generally nocturnal (Lariviere & Walton 1997), diurnal activity is commonly reported (e.g. Taylor et al. 1998, Neale & Sacks 2001, Larrucea et al. 2007). Moreover, Korn and Tewes (2009) have proposed that bobcat populations in Texas may cycle in semi-arid environments due to significant drought-induced declines of sigmodontine rodents (e.g. Sigmodon hispidus), which as I present here are among the most important prey items for jaguarundis.

As the jaguarundi is a mesocarnivore, it is not unreasonable that a diverse guild of larger reptilian, mammalian, and avian predators may occasionally kill and/or consume jaguarundis. For example, Monroy-Vilchis et al. (2011) observed an adult male jaguarundi in the process of being consumed by an adult boa constrictor in Sierra Nanchititla Natural Reserve, Mexico. Still, in their examination of 116 records of intraguild predation and/or interspecific killing among Neotropical mammalian carnivores in the literature, de Oliveira and Pereira (2013) mention only two instances of jaguarundis killed by larger mammalian predators; both of these are predation by puma, and were originally reported as occurring in Brazil by Crawshaw (1995) and Martins et al. (2008). In comparison, they collected 11 records of other small Neotropical felids (Leopardus sp.) including ocelots killed by jaguars and pumas, and two records of ocelots killing other small felids.

Many accounts of jaguarundis are of more than one individual, and they are frequently observed in pairs. Rengger (1830) was the earliest to claim that jaguarundis were 'normally encountered in pairs living in well-defined territories', although he made similar claims for ocelots, which have not since been supported. Nevertheless, he also refers to an incident where his dog chased six adult jaguarundis out of a single thicket. Although Mondolfi (1986) personally only observed single jaguarundis, he reported two second-hand observations (by B. Thomas and R. Hoogesteijn) of pairs walking in savanna pasture and small, wooded areas. Of 10 encounters I experienced with jaguarundis in the Dry Chaco and Atlantic Forests of Paraguay, four were with pairs and six with single animals. Most interesting perhaps are two of three detailed observations recounted by McCarthy (1992) in Belize. In one report, the author observed a second jaguarundi join a first on the banks of the Temash River after the first animal failed in stalking a basking iguana. A second more extended encounter in Tikal National Park in Guatemala

involved two jaguarundis that were active in the canopy at night below an area where the author was mist-netting bats. McCarthy (1992) proposed that their frequent occurrence in pairs could be something 'other than young siblings or short-term reproductive courtship'. Little is known about the social habits of free-ranging jaguarundis, and it is unclear if adults sometimes travel in pairs; it is possible that most such observations are of fully grown offspring travelling with mothers. The number of anecdotal jaguarundi observations involving pairs that have been reported however, along with several reports of jaguarundi activity or resting in trees at night, could be further adaptations facilitating the co-occurrence of a diurnal, tropical forest predator with several terrestrial, nocturnal predators of similar or larger size. Future direct studies of jaguarundis might permit further exploration of these intraspecific interactions.

ANTHROPOGENIC THREATS AND STATUS

Jaguarundis never suffered the fate of many spotted cat species that were targeted during the widespread fur trade decades ago (Broad 1987). Today, although they are still probably the most widely distributed small felid in the western hemisphere (de Oliveira 1998a, Caso et al. 2008), jaguarundis are hunted locally for various reasons. Local communities among the Sierra Nanchititla forests of Mexico reportedly harvest jaguarundis for alleged medical and ornamental purposes (Monroy-Vilchis et al. 2008), and similar practices appear to occur in the Yucatan Peninsula (Santos-Fita et al. 2012).

A more widespread local threat to jaguarundis from local communities may be due to their tendency to prey upon poultry. Reports of depredations are common from Mexico and Brazil (e.g. Sanchez et al. 2002, Michalski et al. 2006, Monroy-Vilchis et al. 2011) and are likely to be widespread throughout the Neotropics. Early accounts from Paraguay describe jaguarundis stalking domestic chickens and their habit of taking sleeping hens at night from the trees (Rengger 1830). In Belize, Rabinowitz (1984) claimed that jaguarundis were a fairly frequent depredator of chickens of local indigenous groups; people found them challenging to shoot in retaliation. McCarthy (1992) received numerous reports of jaguarundis as pests in rural, remote Belizean villages, including complaints of jaguarundis killing chickens, and confirmed at least two instances of conflict where farmers shot and skinned jaguarundis after such depredations. In Chiapas, del Toro (1977) considered the jaguarundi to be an important pest of poultry, and described incidents involving both individuals and pairs that devastated coops of hens, turkeys, etc. More recent findings in the same region (Lacandona) suggested that jaguarundis were more frequently involved in livestock-related conflict than

jaguars, pumas, ocelots, and margays (Garcia-Alaniz et al. 2010), possibly reflecting a higher tolerance to human development. Domestic chickens were also recorded from the stomachs of road-killed jaguarundis in Venezuela, and there is an account from the country of an adult male killed in pursuit of a turkey in the poultry house of a local college (Bisbal 1986, Mondolfi 1986).

Throughout their range, it is unclear how large-scale transformation and conversion of habitat is impacting jaguarundis. Most of the evidence collected here is consistent with the claim that jaguarundis occupy and use secondary and gallery forest habitats, small forest fragments, and mixed agricultural/plantation (e.g. Eucalyptus) landscapes in diverse geographical regions, including southern and western Mexico, Belize, Atlantic forest in southern Brazil and eastern Paraguay, and the Gran Chaco of Paraguay, Bolivia, and Argentina. It is possible that jaguarundis exist at lower densities than has traditionally been believed, due to competitive exclusion and intraguild interactions with larger predators such as ocelots (de Oliveira et al. 2010). However, this idea may be strongly based on original data collected from intact primary forest in the Brazilian Amazon, a region lacking dense shrub or thicket cover, an important factor influencing the presence of jaguarundis on the landscape (Quibrera 2011). Mondolfi (1986) believed that jaguarundis were still relatively common throughout Venezuela, and did not see deforestation as a major threat to them, due to their ability to find cover in thickets and shrubs and to persist in agricultural landscapes. In contrast, De Almeida et al. (2013) considered habitat loss due to agricultural expansion in Brazil the greatest threat to the species.

In a landscape mosaic of intensive deforestation in the southern Amazon (Mato Grosso), Michalski and Peres (2005) reported that jaguarundis occupied a greater proportion (53%) of forest fragments (n = 129) than ocelots (38%), jaguars (33%), and pumas (28%), perhaps due to the cover afforded by the thick undergrowth in and surrounding disturbed forests. Mean forest fragment size occupied by jaguarundis (7.9 km²) was also smaller than for ocelots (mean = 11.11 km^2), pumas (mean = 13.72 km^2), and jaguars (mean = 13.08 km^2). Stone et al. (2009) also reported on the ability of jaguarundis to use very small Atlantic Forest fragments. Jaguarundi occupancy in Upper Parana Atlantic Forest fragments did not appear to be affected by the level of protection afforded to an area, and increased sampling effort did not result in an increased probability of their detection (Di Bitetti et al. 2010). In contrast, protection category was important to jaguars, pumas, and ocelots, while greater sampling effort generally led to increased detection probability for jaguars, pumas, ocelots, margays, and oncillas (Di Bitetti et al. 2010).

Whereas the number of ecological investigations of Neotropical carnivore assemblages appears to be increasing, studies of jaguarundis specifically are lacking. Details therefore on how interacting factors such as habitat suitability, land use type and intensification, fragmentation, land protection status, and interference competition impact jaguarundis remain relatively little known. As a consequence, whether populations are relatively stable or declining is also unknown. That jaguarundis have frequently been reported from agricultural areas and small forest fragments suggests a possible adaptation to humanmodified landscapes, particularly in the absence of predators or competitors, or at least, lower densities of these species. The presence of jaguarundis in such habitats may also be related to the greater abundance of sigmodontine and avian prey, which might find secondary vegetative growth and/or dense shrub and thicket layers more favourable. In Southeast Asia, leopard cats Prionailurus bengalensis appear to occupy a similar niche, exhibiting a greater preference for human-modified landscapes (e.g. oil palm plantations, logged secondary forest) than their larger sympatric competitors (Rajaratnam et al. 2007). Ultimately, because little research has been conducted on jaguarundis, more regional surveys of its status, and local population monitoring efforts in different landscape contexts, are urgently recommended to ascertain if its conservation status should remain 'Least Concern' (Caso et al. 2008), or if a change is warranted.

CONCLUSIONS

The jaguarundi is the most widely distributed small felid in the western hemisphere. It appears to inhabit areas in the vicinity of very dense undergrowth spanning a variety of tropical habitats, including thornscrub, dry seasonal forest, gallery forest, Atlantic Forest, and Chaco semi-arid scrub forest. Some anecdotal accounts and one telemetry study suggest that the jaguarundi may be associated with riparian areas in and around forests, particularly in tropical seasonal forests; however, more scientific studies are needed on the subject. Multiple studies suggest that it is also very capable of making use of small forest fragments and mixed agricultural landscapes.

Based on the evidence reviewed here, jaguarundis are largely predators of small mammals, particularly rice and cotton rats (larger sigmodontine rodents), which may be more prevalent in agriculturally modified landscapes. Their diet also includes smaller mice, small and larger opossums, cavies, rabbits, and occasionally larger mammals such as paca. Birds also appear to be important prey; although little effort has been made to identify bird prey in detail. Among non-domesticated bird species, those most typically associated with dense undergrowth (doves, tinamous, etc.) appear to be prey, and in some areas, they might be as important as mammals in the diet of jaguarundis. Lizards are also common prey, and insects appear to be taken frequently and opportunistically in some locations.

Jaguarundis appear to be largely diurnal, possibly to avoid encounters with other predators or competitors; pre-dawn, evening, and overnight activity has been recorded by observers however, and this is also supported by camera-trap and telemetry-based studies. Despite a few reports of jaguarundis in trees at night and their purported skills at climbing, they appear to be nearly exclusively terrestrial in their habits. Jaguarundis may occupy a dietary niche more aligned with those of margays and oncillas than with that of ocelots, as the greatest similarities in prey selection and niche overlap appear to occur with these species. Ocelots could be important factors influencing the presence, activity, and/or abundance of jaguarundis in an area; alternatively, the diurnal habits of jaguarundis may facilitate coexistence with ocelots with little direct competition between the two, although research is needed across more habitats and ecological contexts to better assess this relationship. Home ranges of individual jaguarundis appear to vary widely throughout their geographical range, although most animals studied ranged over $\leq \sim 20-25$ km². The home ranges of males were slightly larger to much larger than those of females across different areas, and significant intersexual and intrasexual overlap can occur.

While evidence of humans directly hunting jaguarundis appears to be uncommon, mortalities due to retaliation for depredating poultry may be more common and widespread than is believed, particularly in expanding agricultural areas. This could be exacerbated by the disappearance of larger predators from these same areas, although conflict does not appear to be exclusive to this scenario (e.g. Garcia-Alaniz et al. 2010). Inskip & Zimmerman (2009) concluded that conflict perpetrated by smaller felids has been the subject of few formal investigations and is therefore probably under-reported; I recommend more focused research on this issue.

Finally, the lack of information regarding the jaguarundi's status throughout its range is of concern. Aside from Caso (2013), few field researchers have explicitly focused on the jaguarundi. Given that populations of many Neotropical felids are declining due to habitat loss, addressing this concern should be a priority. Broad-scale surveys to identify local areas of jaguarundi abundance, long-term population monitoring, and studies investigating the habitat needs of the species in the context of competitive interactions would greatly improve our understanding of the cat species' needs, and thus should be a priority.

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