



Figure 1 – Selected sites to trap *Abrothrix olivacea* in the Coastal Maulino Forest. Black: the native forest; grey: the young pine plantations; white: the adult pine plantations. NF: native forest, YPNU: young pine plantation with a scarce or null understory; YPWU: young pine with an abundant understory; and AP: adult pine with an abundant understory.

replacing the native forest with *P. radiata* plantations (Echeverría et al., 2006). Two large native forests have been retained: the Los Queules National Reserve and Los Ruiles National Reserve. Pine plantations are usually associated with low amounts of organic matter and soil humidity, which are caused by low absorption and higher water consumption, as the soils in these regions are drier than those of the native forest (Huber et al., 2008; Hofstede et al., 2002; Fahey and Jackson, 1997). One of the strategies used to mitigate the effect of habitat change in plantations is the integration of an understory, as the understory can serve as a substitute habitat for some organisms (Simonetti et al., 2013). Only one parasitological study has been conducted in this area, which compared the abundance of *Eutrombicula alfreddugesi* parasitising *Li-oalemus tenuis* at the border of the continuous native forest and the native patches within its interior (Rubio and Simonetti, 2009). Thus, the impacts of anthropic activities on the parasites of mammals in the Coastal Maulino Forest have not been studied. *Abrothrix olivacea* is a mammal with one of the most extensive distributions in Chile; it is found in a wide variety of environments, such as at sea level to 2500 m above sea level (Iriarte, 2008). This mammal tends to be active at night and during twilight, and it generally nests in dens, trunks, or rocks (Mann, 1978). The present study thus aimed to assess the association between habitat type, season, host density, host sex, and the host's body condition on the presence and abundance of two taxa of mites that parasitise the rodent *Abrothrix olivacea* (Cricetidae).

One of the mites being studied is *Ornithonyssus* sp. (Mesostigmata); it belongs to Macronyssidae which are obligate haematophagous species that inhabit the nests of hosts and only make contact with the host when a blood meal is necessary. The other mite is *Androlaelaps* sp. (Mesostigmata), which is a group of species that also inhabit the nests of hosts. The latter can either reproduce successfully by feeding on arthropods, or they may also feed on blood as part of their diet; the remainder of this parasite's diet can include secretions from tears, scabs, small arthropods, and the faeces of fleas (Krantz and Walter, 2009; Dowling, 2006).

This study considered different habitat types — the native forest (NF) and pine plantations — which were sub-grouped as an adult pine plantation with an understory (AP), a young pine plantation with an abundant understory (YPWU), and a young pine plantation with a scarce or null understory (YPNU).

Materials and Methods

This study was conducted in the Los Queules National Reserve (35°59'119" S, 72°41'15" W) and in the pine plantations surrounding the reserve (Fig. 1. See Donoso et al., 2004 for further details of the location). Three sites, separated by at least 400 m, were selected within each of the four previously mentioned habitat types (a total of 12 sites). A 60×90 m grid with 70 live traps (Sherman®; placed at 10 m distances relative to each other) was set in each site over the course of four consecutive nights (the traps were kept inactive during the day) during each season from autumn of 2016 to summer of 2017. To avoid tem-

poral bias, sampling was carried out each season, where trapping was performed simultaneously across the four different habitat types. Specifically, trapping was conducted for four consecutive nights at each of the three chosen sites (each seasonal trapping session took 12 nights). Rodents were anaesthetised within a bag containing 0.4 mL of isoflurane (USP, Baxter) and put on a piece of cotton within a tea infuser. Then, the rodents were ear tagged, measured, weighed, and their sexes were recorded. After that, any ectoparasites were carefully extracted and kept in 70% ethanol in 2 mL microtubes. Finally, the rodents were released in the same place they were captured.

Mites were cleared in Nesbitt and mounted in Berlese solution (Krantz and Walter, 2009). Mites other than those belonging to the *Ornithonyssus* and *Androlaelaps* genus were not considered given their very low prevalence and abundance.

The terms “prevalence”, “abundance”, and “mean abundance”, as related to parasites, were used in line with the definitions of Bush et al. (1997). Confidence intervals are given for the prevalence rates. Given the aggregate and asymmetrical distribution for parasite abundance, the median and interquartile range are given with the mean abundance. Rodent body condition was calculated using Fulton's K factor, where:

$$K = 100 \cdot \frac{\text{weight}}{\text{total length}^3}, \quad (1)$$

with the weight of each host expressed in grams and the total length in centimetres. Host density was estimated per grid within a season, following Schnabel's 1938(1938) second method:

$$N = \frac{\sum t_i M_i}{-\sum r_i}, \quad (2)$$

where N is the estimated number of rodents in the studied area, t_i is the number of rodents captured in the i^{th} night, M_i is the number of tagged rodents at the start of the i^{th} night, and r_i is the number of re-captured rodents in the i^{th} night.

For this estimation, recaptures only included those rodents that were captured previously in the same season; rodents captured only in previous seasons were considered as first captures.

Multifactorial logistic regressions were performed to assess the association between the presence of mites and the independent variables (habitat type, season, estimated host density, host sex, host body mass, and the host's body condition). To assess the association between the same independent variables and the abundance of mites, multifactorial negative binomial regressions were performed. In both cases, the best models were selected using likelihood ratio tests (LR-tests). The variable with the highest p -value was considered non-significant and was removed if there was no significant loss of likelihood by removing it. Given that body mass and body condition are not independent variables, they were separately assessed in different regression models. Thus, two complex models were initially assessed to determine the variables associated with either the presence or abundance of parasites in each mite species. Given that the negative binomial regression models examined the total abundance and not the mean abundance, we used the term “abundance” for the analysis and discussion. Likewise, given that the logistic regression models explored parasite presence and not prevalence, we used the term “presence” for the analysis and discussion. Statistical analyses were performed using Stata II S.E. (StataCorp LLC, College Station, TX, USA).

All animal procedures were approved by the Bioethics Committee of the Faculty of Veterinary Sciences of the University of Concepción (code CBE 29-2017). Captures were approved by the National Forest Corporation (permit number 04-2015) and Agricultural and Livestock Service (permit number: 6831/2015).

Results

A total of 2445 *Ornithonyssus* sp. and 182 *Androlaelaps* sp. were collected from 484 rodent captures. Among all rodents, the prevalence of *Ornithonyssus* sp. was 70.87% (confidence interval [CI]: 66.81–74.93) and that of *Androlaelaps* sp. was 16.1% (CI: 12.8–19.4). The partial mean abundance and prevalence are shown in Tab. 1.

Table 1 – Mean estimated density of *Abrothrix olivacea*, prevalences (95% confidence interval) and mean abundances (Median / interquartile range) of mites (by taxon) by season, and type of habitat in the National Reserve Los Queules and surrounding pine plantations.

Season	Type of habitat ¹	Mean estimated	Number of examined hosts per habitat	<i>Ornithonyssus</i> sp.				<i>Androlaelaps</i> sp.			
		<i>A. olivacea</i> per grid		Prevalence (%)	Prevalence (%)	Mean abundance	Mean abundance	Prevalence (%)	Mean abundance	Mean abundance	
Autumn 2016	NF	3	7	42.9	9.9–81.6	1	0/0-2	14.3	0.4–57.9	0.1	0/0-0
	AP	14.5	23	65.2	42.7–83.6	3	2/0-6	13	2.8–33.6	0.6	0/0-0
	YPWU	54.7	99	89.9	82.2–95	8.9	7/3-14	2	0.2–7.1	0.0	0/0-0
	YPNU	13.8	35	88.6	73.2–96.8	4.3	2/1–6	20	8.4–36.9	0.8	0/0-0
Winter 2016	NF	3.7	9	11.1	0.3–48.2	0.1	0/0-0	11.1	0.3–48.2	0.2	0/0-0
	AP	7.9	13	0	0–24.7	0	0/0-0	23.1	5–53.8	0.4	0/0-0
	YPWU	27.2	50	36	22.9–50.8	0.6	0/0-1	30	17.9–44.6	0.6	0/0-1
	YPNU	8.1	12	25	5.5–57.2	0.3	0/0-0.5	41.7	15.2–72.3	1.1	0/0-2
Spring 2016	NF	0	0	-	-	-	-	-	-	-	-
	AP	3	3	100	29.2–100	2	2/2-2	66.7	9.4–99.1	1.7	2/0-3
	YPWU	29.3	75	81.3	70.7–89.4	8.6	3/1-9	25.3	16–36.7	0.5	0/0-1
	YPNU	8.1	18	88.9	65.2–98.6	3.6	1/1-2	33.3	13.3–59	1.1	0/0-1
Summer 2017	NF	1	2	0	0–84.2	0	0/0-0	0	0–84.2	0	0/0-0
	AP	3.9	7	71.4	29–96	4.2	4/0-6	0	0–41	0	0/0-0
	YPWU	63.2	89	83.1	73.7–90.2	5.3	4/1-7	10.1	4.7–18.3	0.2	0/0-0
	YPNU	39.6	42	57.1	41–72.3	2.1	1/0-3	11.9	4–25.6	0.2	0/0-0

¹ NF: native forest, AP: adult pine plantation with abundant understory, YPWU: young pine plantation with abundant understory, and YPNU: young pine plantation with scarce understory.

Ornithonyssus sp.

In the best model, habitat type and season were significant factors for the presence of *Ornithonyssus* sp., as the prevalence of this species was higher in YPWU (odds ratio [OR] =11.7, $p<0.01$) and YPNU (OR=6.8, $p<0.01$) than in NF (see Tab. S1, for the full output of the best model). The host's body mass, body condition, sex, and estimated density were not significant. On the other hand, habitat type, season, and host sex were significantly associated with the abundance of *Ornithonyssus* sp., as the abundance of this species was higher in YPWU (coefficient [Coef]=2.32, $p<0.01$), AP (Coef=1.19, $p=0.03$), and YPNU (Coef=1.39, $p=0.01$) than in NF (Tab. S2). Body mass, body condition, and estimated density were not significant.

Androlaelaps sp.

Season was the only significant factor associated with the presence of the *Androlaelaps* sp. (Tab. S3). Habitat type, as well as the host's body mass, body condition, sex, and estimated density, were not significant. When analysing the abundance of this parasite species, both season and habitat type were significant factors in the best model, and the likelihood of this model (log[likelihood]=-310.9) was significantly higher than in the model that did not feature "habitat type" as a factor (log[likelihood]=-315.8; LR-test: $p=0.012$); however, none of the habitat types showed a coefficient that was significantly different from 0 (see Tab. S4). Given that, we also compared both models with Akaike's criterion, and the results also suggested that a more complex model should be used (two-factor — season and habitat type — model AIC=636.6; one-factor — season — model AIC=641).

Given the results of the last model, we explored it further to determine whether there were significant associations between the presence and abundance of mites with habitat type (other than NF), particularly in the two young pine plantations. Thus, when only the young pine plantations (YPWU and YPNU) were included in the analyses — and, thus, the abundance of the understory was the most important difference between habitats — habitat type and season were found to be significant factors for the presence of *Ornithonyssus* sp., which had a higher prevalence in YPWU (OR=1.85; $p=0.03$) than in YPNU (Tab. S5). The other variables were not significant. Similar to what was found for prevalence, both habitat type and season were found to be sig-

nificant factors for parasite abundance: specifically, the abundance was higher in YPWU than in YPNU (Coef=0.93; $p<0.01$). Also, the host's sex was a significant factor (Tab. S6), while the other variables were not significant.

In the case of the *Androlaelaps* sp., mite prevalence and abundance were both significantly lower in YPWU (logistic regression: OR=0.27, $p<0.01$; binomial negative regression: Coef=-1.12; $p<0.01$) than in YPNU; these findings were associated with seasonal variation (Tab. S7 and S8). Host density was also positively associated with the presence of the *Androlaelaps* sp. (OR=1.02; $p=0.05$). The other variables were not associated with the abundance or prevalence of this parasite species.

Discussion

Both the prevalence and abundance of the *Ornithonyssus* sp. varied when the native habitat was substituted by pine plantations. Variation in the prevalence and abundance of *Ornithonyssus* was associated with the host's habitat type, as reported previously in the literature. A study from Buenos Aires (Argentina) that was conducted in protected (a mixture of graminoid swamps and forested wetlands) and unprotected (frequently flooded scrublands, and xeromorphic and riparian marshlands along the riverbanks) areas found different abundance levels of *O. baccoti* (among other ectoparasites), which were attributable to the environmental differences between localities (Lareschi and Krasnov, 2010).

Conversely, the presence and abundance of *Androlaelaps* sp. did not show a significant association with habitat type (i.e., when comparing NF with the three plantations), which can be attributable to the biological traits of the mites of this genus, which do not need to remain on their hosts for very long (Krantz and Walter, 2009). Thus, the development and survival of these mites can be affected by the conditions of their microhabitats, as represented by the rodents' dens. Further, the micro-climate within dens can be different from the climate that is external to them (Furman, 1968).

The differences in the prevalence and abundance trends observed between the various habitat types for *Ornithonyssus* sp. and *Androlaelaps* sp. suggest that *Ornithonyssus* sp. spend more time on the host than do *Androlaelaps* sp. This is in agreement with the fact that *Orni-*

thonyssus only feeds on the host's blood, while *Androlaelaps* also feeds on other substrates (Dowling, 2006).

Regarding seasonality, some studies have reported a null effect of this variable on the presence and abundance of *O. bacoti*, except there are changes in seasonal variation that affect host density (Soliman et al., 2001). In the present study, there was no evidence that host abundance caused the seasonal variation that were observed for the parasite's presence and abundance. The fact that seasonality was a significant factor in the variability of the presence and abundance of both mite species may be due to the idea that seasonality simultaneously affects all types of habitats, including the den's interior, as seen in Furman (1968).

When considering the abundance of the understory, the models explored in this study considered only YPWU and YPNU. It was found that habitat type was a significant factor that influenced the presence and abundance of both mite species. Specifically, *Ornithonyssus* sp. showed higher prevalence and abundance levels in habitats with an abundant understory than in habitats with a scarce or null understory; this is likely due to the fact that understories typically feature lower sun radiation, higher humidity, and more regulated temperatures (Zhao et al., 2014). However, this finding is not consistent with the lower abundance levels and prevalence of this mite in NF, where solar radiation and temperature typically remain constant. Conversely, *Androlaelaps* sp. showed lower prevalence and abundance levels when the understory was abundant than when it was scarce or null. Further studies exploring the optimal environmental conditions for both mite species, and those investigating how the understory affects the den's environment, could explain this result.

As far as we know, this is the first study to compare the presence and abundance of mesostigmatid parasitic mites between habitats featuring an abundant and scarce understory in forestry plantations. However, the results presented here must be taken carefully, as understory coverage was not measured and the detailed ages of the young plantations were not assessed (of note, however, the YPWU had a more abundant understory than did the YPNU, and young plantations were younger than AP). Other studies assessed the effect of the understory on free-living arthropods species, which confirmed that the removal of the understory is associated with lower species richness and arthropod density (Bokhorst et al., 2014; Hasegawa et al., 2013; Zhao et al., 2013; Materna, 2004).

The lack of an association between the host's body mass, body condition, and either the presence or abundance of both mite species is in agreement with the findings of previous studies (Schlaepfer, 2006; Figuerola, 2000). Postawa et al. (2014) found an association between parasite abundance and the host's body condition while only considering highly infected hosts; conversely, in the present study, there were no highly infected hosts, as the highest intensity was 63 mites, which can explain the lack of an association between both variables. The role of the host's body condition on parasitic load is controversial given that the former can be either the cause or the consequence of high parasitic loads. Thus, in addition to the aforementioned studies, researches reporting both negative (Lourenço and Palmeirim, 2007) and positive (Sánchez et al., 2018; Rajemison et al., 2017) associations have also been published. However, studies of parasites that focussed on habitat alterations, while considering the host's body condition and mass, are scarce. Another work that explored a similar relationship was that of Froeschke et al. (2013), but the authors examined habitat fragmentation and host body length.

The higher abundance of *Ornithonyssus* sp. observed in male hosts when compared with female hosts is in agreement with the findings of many previous studies, and has also been explained by several hypotheses as the behavioural, body mass, and hormonal/immunological differences between male and female hosts (Kiffner et al., 2013; Krasnov et al., 2012; Harrison et al., 2010). Neither behavioural nor hormonal/immunological differences were assessed in this study. Nevertheless, there were no associations with body mass that could explain the sex differences in the parasitism of *Ornithonyssus* sp. On the other hand, the lack of an association between the presence or abundance of *Androlaelaps* sp. with host sex was previously reported in this genus

(Lareschi, 2006). A possible cause is that the behaviour of male hosts (aggressivity and movement, for instance) is not important in the transmission of parasites, as transmission occurs in the nest or within the den (Krantz and Walter, 2009).

The lack of an association between host density — after correcting for habitat type and season — with either the presence or abundance of *Ornithonyssus* sp. and *Androlaelaps* sp. contrasts with the results of previous studies that found a positive association between these factors (Ancillotto et al., 2018). One report found an association between the abundance of *O. bacoti* with seasonal variation in host density, but only during some seasons (Soliman et al., 2001). Our results can be explained by either a real lack of importance of host density, or by the presence of alternative hosts (rodents) present in the studied geographic area, such as *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *Phyllotis darwini*, *Irenomys tarsalis*, *Geoxus valdivianus*, *Ocotodon bridgesi*, and *Rattus rattus* (Correa and Roa, 2005; Saavedra and Simonetti, 2005). Although these rodents were not considered in this study due to the very low number of captured specimens, they could represent several types of hosts that are large enough to exert a host-density effect. Although this lack of association is not new, studies that have assessed this association — while controlling for other variables, including host sex, locality-associated factors, and seasonal variability — are not common, and they have also noted that the same variables that affect parasite density can affect host density (Chan et al., 2016; Sunyer et al., 2016).

Thus, this study provides evidence to indicate that the effect of environmental disturbances, particularly the replacement of native forests by pine plantations, can have different impacts on each parasite species. Further, this study also highlights how different forestry management approaches can have different effects on parasites. Given that parasites can affect host populations (Hudson et al., 1998), changes in parasite populations can lead to changes in host populations, thus affecting the whole community. Our results suggest that habitat alterations can affect parasitism rates, but differently among parasite species. Thus, it is necessary to study the changes in each parasite species while being cautious to avoid extrapolating the findings of one parasite to another. Considering that parasites constitute an important part of our ecosystems, the results of our study underline the need to incorporate parasites in studies that explore the impacts of environmental disturbances. By doing so, we may be able to avoid pushing parasites to extinction or, conversely, converting them into a plague that threatens various host populations.

Finally, many mite species, including *Ornithonyssus* species, are vectors for diseases (Bhate et al., 2017). Thus, the study of the changes in mite populations due to the effect of environmental alterations is important to understanding the epidemiology of those diseases. ☞

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Supplemental information

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

- Table S1** Parameters of the logistic regression model “Presence of *Ornithonyssus* sp. = season + type of habitat”.
- Table S2** Parameters of the negative binomial regression “Abundance of *Ornithonyssus* sp. = season + type of habitat + sex”.
- Table S3** Parameters of the logistic regression model “Presence of *Androlaelaps* sp. = season”.
- Table S4** Parameters of the negative binomial regression “Abundance of *Androlaelaps* sp. = season + type of habitat”.
- Table S5** Parameters of the logistic regression model “Presence of *Ornithonyssus* sp. = season + type of habitat”.
- Table S6** Parameters of the negative binomial regression model “Abundance of *Ornithonyssus* sp. = season + type of habitat + sex”.
- Table S7** Parameters of the logistic regression model “Presence of *Androlaelaps* sp. = season + type of habitat”.
- Table S8** Parameters of the negative binomial regression model “Abundance of *Androlaelaps* sp. = season + type of habitat”.