

# The Role of Sex and Mating Status in the Expansion Process of *Arhopalus rusticus* (Coleoptera: Cerambycidae)—an Exotic Cerambycid in Argentina

Mariano Pablo Grilli<sup>1</sup> and Romina Fachinetti

CREAN (IMBIV) – CONICET – Universidad Nacional de Córdoba, Av. Valparaíso S/N - Ciudad Universitaria, Córdoba, Argentina (mariano.grilli@unc.edu.ar; rominafachinetti@gmail.com), and <sup>1</sup>Corresponding author, e-mail: mariano.grilli@unc.edu.ar

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## Abstract

In Córdoba province, central Argentina, there is an area of introduced pine trees, in which an invading Cerambycid, *Arhopalus rusticus* (L.), was detected in this region for the first time in 2006. The species has since expanded its range until it now occupies the whole area. *Arhopalus rusticus* is a common species in pine forests of the northern hemisphere. In this paper, we analyze how sex and mating status affects flight performance and the potential distribution of this species. The study was performed with individuals collected from introduced pine forests in the center-west of Córdoba Province (Argentina). The dispersal capability of *A. rusticus* was determined by measuring flight speed and distance traveled by recently emerged mated and unmated *A. rusticus* in flight mills. Data of preflight body weight, postflight body weight, body length, and elytron size were obtained from the individuals that were flown in the flight mill. We found that females had a greater body length, weighed more, had longer elytra, and were stronger flyers than males. We also found that mated individuals flew faster and longer distances than unmated individuals, and consumed a smaller fraction of their body weight. A positive ratio was observed between elytra size and flight speed. A map of males' and females' dispersal distances was produced for the study region, using the adjusted dispersal distance distribution of males and females. The flight performance showed that, as females disperse after copulation, they increase the chances of establishing the species in unoccupied areas.

**Resumen** En la provincia de Córdoba, Argentina, hay una importante área de pinos implantados. En esta región durante el año 2006 se detectó por primera vez a *Arhopalus rusticus* (L.), un Cerambycidae invasor. *A. rusticus* es una especie común en los bosques de pino del hemisferio norte. En este trabajo analizamos de qué manera el sexo y el estado de apareamiento afectan el desempeño de vuelo y la distribución potencial de esta especie. Utilizamos individuos recolectados de los bosques de pino implantados en la región centro oeste de la provincia de Córdoba (Argentina). La capacidad de dispersión de *Arhopalus rusticus* se determinó haciendo volar individuos recién emergidos en un molino de vuelo. Se registró el peso previo y posterior al vuelo, el largo del cuerpo y el tamaño del élitro. Las hembras fueron mejores voladoras, más largas, más pesadas, con élitros más largos que los machos. Observamos diferencias entre el potencial de dispersión dependiendo del estado de apareamiento de los individuos. Los individuos apareados volaron más rápido y mayores distancias que los individuos no apareados y consumieron una menor fracción de su peso corporal. Se observó una relación positiva entre el tamaño del élitro y la velocidad de vuelo. Se generó un mapa de las distancias de dispersión potencial de los machos y de las hembras para la región de estudio utilizando las distribuciones de las distancias obtenidas del molino de vuelo. La dispersión post copulación incrementa las chances de que la especie se establezca en zonas no ocupadas.

**Key words:** *Arhopalus rusticus*, flight mill, dispersal, invasion, exotic

In the early 1940s, 24,000 hectares of the introduced pine species *Pinus elliotii* and *Pinus taeda* were planted in the central west region of Córdoba province (Argentina; Censo Nacional

Agropecuario, Instituto Nacional de Estadísticas y Censos de la República Argentina [CNA INDEC], 2002). These two pine species were chosen as they were seen to be the most versatile and best

adapted to this semiarid region (Izurieta et al. 1993). The cultivated woodlands form discrete patches, interspersed in a matrix dominated by natural pastures and shrublands.

During 2006, an invading species of Cerambycidae, *Arhopalus rusticus* (L.), was detected in this area for the first time (López et al. 2007). *Arhopalus* (Cerambycidae: Aseminae) is a Northern Hemisphere genus with about 25 species and subspecies whose larvae develop in coniferous trees (Villiers 1978) and which is present in all major biogeographic regions of the world through the spread of trade (Özdikmen 2014). *Arhopalus rusticus* is a common species of cerambycid in pine forests of North America, Central and Northern Europe, Siberia, Korea, Mongolia, Japan, North China, and North Africa (Furniss and Carolin 1977, Kolk and Starzyk 1996, Wang and Leschen 2003, Özdikmen 2014), and was later introduced in Australia and the Neotropical Region (Özdikmen 2014). The species is mainly found in conifers of the genus *Pinus*, but can attack other conifers such as *Picea*, *Abies*, *Larix*, *Cupressus*, *Cryptomeria*, and *Juniperus* (Jurc et al. 2012, Özdikmen 2013). The larvae mainly infest the roots and the base of the stems of healthy, stressed or dead trees, and occasionally damage structural timbers (Rassati et al. 2012, Özdikmen 2013). *Arhopalus rusticus* individuals arrive in new patches, dispersing from previously infested patches. The dispersal of these insects between patches is a key process in the regional dynamics of their populations (Cronin 2003, Grilli et al. 2015).

Dispersal is defined as the movement of an organism from one location to another (Clobert et al. 2001), and is crucial for the persistence of populations (Johst et al. 2002).

Dispersal should not be considered a fixed trait of a species, but as an individual trait with particular variation both within and among populations, according to various selective pressures (e.g., Clobert et al. 2004, Van Dyck and Baguette 2005).

Differences in dispersal ability are observed among populations of the same species living in different environments (Hanski et al. 2004, Mennechez et al. 2004, Schtickzelle et al. 2006), and among different individuals of the same population (Barbaresi et al. 2004, Doerr and Doerr 2005). A good knowledge of the characteristics of individuals that affect their dispersal capacity should facilitate understanding of the spatial dynamics of an invading species.

One way of gaining knowledge of the dispersal capacity of a species is by comparative studies conducted in the laboratory under controlled conditions. For flying insects, these comparative studies are usually carried out using tethered flight experiments, attaching the individuals to a flight mill (Ranius et al. 2005). Sex, body condition, and mating status are factors that may influence dispersal capacity in insects (Ims and Hjermann 2001, Dubois et al. 2010). For example, food deprivation increased flight activity in *Prostephanus truncatus* Horn (Coleoptera: Bostrichidae) (Fadamiro et al. 1996), but suppressed flight activity in *Tetraopes tetrophthalmus* Forster (Coleoptera: Cerambycidae) (Davis 1984). The latter showed a sex-biased dispersal behavior, with the females flying longer distances than the males (Davis 1986). Unmated females of *Monochamus carolinensis* (Coleoptera: Cerambycidae) outperformed their mated counterparts on all measures of flight (Akbulut and Linit 1999), but this is not the case in *Trirhabda virgata* (Coleoptera: Chrysomelidae) in which the only dispersing females are the mated ones (Herzig and Root 1996).

The central west region of Córdoba Province (Argentina) has the largest implanted pine area of central Argentina. This area is isolated from the main pine production region of the country, which is in Misiones Province 1,000 km away. There are no reports as yet of the presence of *A. rusticus* in any other pine production region of

the country. Understanding the dispersal mechanisms and invading dynamics of this species is key to developing any management program.

Since *A. rusticus* was first observed in this region, the range of the species has extended, now occupying all the pine patches in the area. In this paper, we proposed to analyze the flight performance of mated and unmated males and females of *A. rusticus* and how this performance can affect the distribution of this species.

## Materials and Methods

The study was performed in the center-west of Córdoba Province (Argentina), in an area ranging from 31° 33'30" S, 64° 54'19" W in the north, to 32° 33'00" S, 64° 36'55" W in the south. This is the main pine production region of the center of the country (Fig. 1). The study area is mainly mountainous, dominated by shrublands and high altitude grasses with exotic pine forests of *Pinus taeda* and *P. elliotii*. The annual rainfall is 1,000 mm and the mean annual temperature is 17.9°C (Jarsún et al. 2006).

To analyze the potential dispersal ability of *Arhopalus rusticus*, we collected 70 recently emerged individuals (38 females, 26 mated and 12 unmated; and 32 males, 23 mated and 9 unmated) from logs randomly selected in the field from the whole study area. Four biometric traits of mated and unmated males and females were measured: preflight body weight (mg), postflight body weight (mg), body length (mm), and elytron size (mm). Logs were kept in cages and plastic cups were placed in the pupal emergence hole to prevent individuals mating in the cage. Later in the lab, some of the emerged males and females were placed for 24 h in pairs to copulate. Later, these individuals were measured and placed in flight mills, and allowed to fly for 8 h. Unmated individuals were left alone for 48 h and then placed in the flight mill.

We employed a flight mill based on the model described by Bruzzone et al. (2009), consisting of a wooden box with a holder placed in its center for a vertical needle. The needle was supported by the magnetic field generated by two neodymium magnets. A light horizontal wooden rod was attached to the needle (off-centered) and adult cerambycids were glued by the thorax, using cyanoacrylate glue, to one end of the balanced wooden rod with an entomological pin of 4 cm. *Arhopalus rusticus* individuals were placed at 6 cm from the axis, resulting in a rotational length of 36.68 cm. As mentioned, the mills were placed inside wooden boxes within a closed room with controlled temperature (25 °C). The rotation of the mills was recorded using an infrared optical sensor connected to a computer. Data were recorded using specially compiled software (García 2012) that counted the revolutions per unit of time.

One rotation was recorded each time a beam of a light emitting diode (LED) was interrupted by the tip of the wooden rod opposite to the one where the cerambycid was held. The software recorded every rotation and automatically calculated the total flight distance (m). Distances flown by mated and unmated males and females were compared.

Once the individuals were recovered from the flight mill, a distribution of flight distances achieved by all the mated males and females was generated and the percentage of body weight loss was estimated as the percentage of the difference between the preflight body weight and the postflight body weight. A chi-squared test was employed to test for distribution fitting of the flight distances of both sexes, in order to obtain a dispersal probability function. Later,

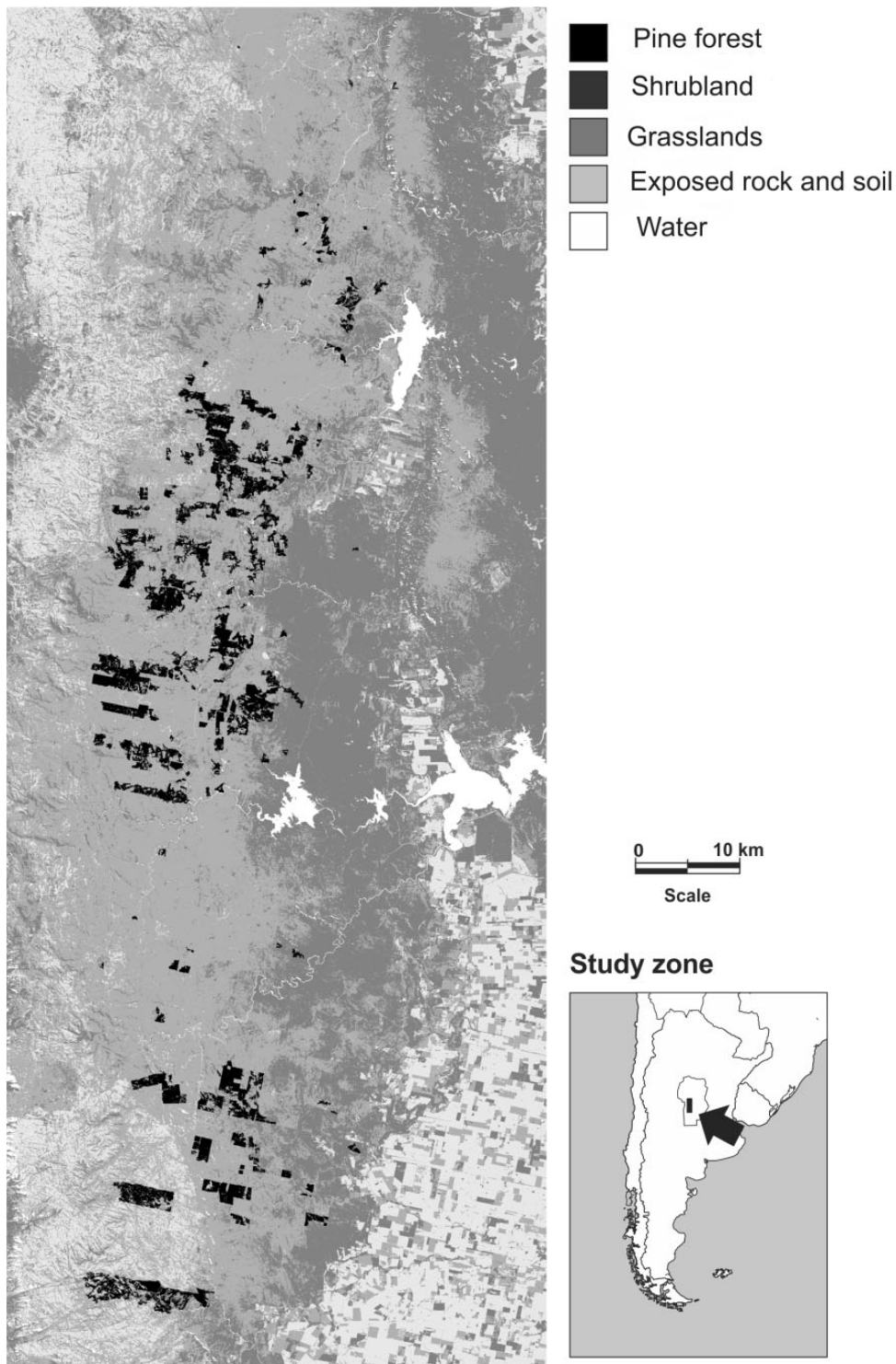


Fig. 1. Study area where pine logs were collected for obtaining the adult *A. rusticus*.

a flight potential map was made using TerrSet GIS software, showing the probability of dispersal from each source pine patch in the study area for each sex based on these probability distributions.

#### Data Analysis

Analyses were conducted using InfoStat Professional v. 2015 (Di Rienzo et al. 2015). All the data were compared using Kruskal–Wallis tests, since residuals did not fit normal distribution.

#### Results

Mated and unmated individuals did not differ in their biometric traits. Mean preflight body weight of mated individuals was 114.8 mg, while for unmated individuals it was 97.3 mg. There was no statistical difference between these two groups ( $H=2.58$ ,  $P=0.11$ ). The same was observed when analyzing body length and elytra length. Mean body length of mated individuals was 16.72 mm, while of unmated individuals it was 17.6 mm.

**Table 1.** Kruskal–Wallis comparison of biometric traits between mated and unmated males and females of *A. rusticus*

Variable	Condition	Sex	N	Mean	H	P
Preflight body weight (mg)	Mated	Female*	26	145	26.30	<0.0001
		Male	23	81		
	Unmated	Female*	12	106	6.10	0.0135
		Male	9	77		
Postflight body weight (mg)	Mated	Female*	26	118	22.45	<0.0001
		Male	23	65		
	Unmated	Female*	12	102	6.10	0.0136
		Male	9	74		
Body length (mm)	Mated	Female*	26	18.38	20.95	<0.0001
		Male	23	14.85		
	Unmated	Female*	12	18.88	4.34	0.035
		Male	9	16.44		
Elytra length (mm)	Mated	Female*	26	12.8	23.99	<0.0001
		Male	23	10.7		
	Unmated	Female*	12	12.3	7.93	0.00045
		Male	9	10.6		

An asterisk indicates significant differences between male and female means. No differences were observed when comparing Mated vs. Unmated.

( $H = 1.29$ ,  $P = 0.25$ ). Elytra length of mated individuals was 11.8 mm, while of unmated individuals it was 11.4 mm. ( $H = 1.61$ ,  $P = 0.20$ ). Comparing the sexes, we found that both mated and unmated females of *Arhopalus rusticus* had a greater body length (mean: mated = 18.38 mm, unmated = 18.88 mm), weighed more (mean preflight body weight: mated = 145 mg, unmated = 106 mg, mean postflight body weight: mated = 118 mg, unmated = 102 mg), and had longer elytra (mean: mated = 12.8 mm, unmated = 12.3 mm) than males (mean body length: mated = 14.85 mm, unmated = 16.44 mm, mean preflight body weight: mated = 81 mg, unmated = 77 mg; mean postflight body weight: mated = 65 mg, unmated = 74 mg; mean elytra size: mated = 10.7 mm, unmated = 10.6 mm; Table 1).

Of the 70 collected, all the mated cerambycids were flown successfully in the mill, but 12 of the unmated did not fly at all. The distance flown by *Arhopalus rusticus* varied between individuals but females of *A. rusticus* were able to fly longer distances. A statistically significant difference was observed between the flight distances and mean flight speed of mated and unmated individuals. Mated individuals showed a mean flight distance of 8006 m, and unmated individuals flew a mean distance of 1612 m ( $H = 22.36$ ,  $P < 0.001$ ; Table 2). Mated individuals showed a mean flight speed of 0.68 m/s, and unmated individuals a mean flight speed of 0.34 m/s ( $H = 17.69$ ,  $P < 0.0001$ ; Table 2). Comparing mated and unmated males and females, we observed that mated females were stronger flyers than males, as they were able to fly longer distances (mated females mean flown distance = 9,655 m, mated males mean flown distance = 6,141 m;  $H = 5.68$ ,  $P = 0.01$ ), and faster (mated females mean flight speed = 0.74 m/s, mated males mean flight speed = 0.63 m/s;  $H = 6.78$ ,  $P = 0.009$ ) than males, but no statistical differences were observed in flight distance and flight speed between unmated males and females (Table 2).

We found a significant difference between mated and unmated individuals in the percentage of body weight loss. While mated individuals lost ~19% of their weight (no difference in weight loss between males and females), unmated individuals lost only 4% of their weight (Table 2).

We also found a positive relationship between elytra length and flying speed ( $R^2 = 0.34$ ,  $P < 0.0001$ ). Flying speed ranged between

**Table 2.** Kruskal–Wallis comparison of flight parameters between mated and unmated males and females of *A. rusticus*

Variable	Condition	Sex	N	Mean	H	P
Flight distance (m)	Mated <sup>a</sup>	Female <sup>b</sup>	26	9655.14	5.68	0.01
		Male	23	4856.84		
	Unmated	Female	12	3383.26	1.17	0.26
		Male	9	524		
Mean flight speed (m/s)	Mated <sup>a</sup>	Female <sup>b</sup>	26	0.74	6.78	0.009
		Male	23	0.63		
	Unmated	Female	12	0.41	1.72	0.17
		Male	9	0.24		
% Weight loss	Mated	Female	26	18.15	0.18	0.67
		Male	23	19.29		
	Unmated	Female	12	4.14	0.01	0.94
		Male	9	3.28		

<sup>a</sup>Indicates significant differences between mated vs. unmated individuals.

<sup>b</sup>Indicates statistical differences observed when comparing male and female means.

0.31 m/s and 0.95 m/s. With their longer elytra, females proved to be faster flyers than males (Fig. 2).

The frequency distribution of distances flown in the flight mill by males and females showed that mated males fitted an exponential model (Chi-square = 2.35,  $P = 0.123$ ) and females a cumulative uniform distribution model (Chi-square = 2.32,  $P = 0.20$ ; Fig. 3).

Using the adjusted probability distribution for male and female dispersal distances, we developed a spatial dispersal probability model for the study area in the TerrSet (Eastman 2015) image calculator. The map of potential probability dispersal obtained showed that mated females have a wider dispersal range than males, being able to reach all the patches in the study area (Fig. 4).

## Discussion

Females of *A. rusticus* have a greater body length, weigh more, and have longer wings than males, regardless of their mating status. Sexual size dimorphism (SSD) is a generalized biological phenomenon in which individuals of one sex are larger than those of the opposite sex (Blanckenhorn 2000). To explain the degree of sexual dimorphism in a species, it is important to consider the variety of factors that can affect the size of females and males (e.g., Andersson 1994, Ralls, 1976). In females, fecundity is the major evolutionary force selecting for larger body size. More precisely, reproductive success increases with body size (Rooff 1992, Stearns 1992, Honck 1993). In males, larger body size increases their mating success, due to intrasexual competition for females (Anderson, 1994). When these major selective pressures affect the sexes in a particular species differentially, sexual size dimorphism results (Blanckenhorn 2005).

But females of *A. rusticus* not only have a greater body length than males but also have a different dispersal potential than males, at least mated ones. We observed that mating status has an effect on flight potential and the strategy of energy consumption. Unmated individuals flew significantly less than mated individuals, especially females. We found that mated females of *A. rusticus* are faster flyers than males and are able to fly almost twice the distance flown by males, which will eventually produce a differential dispersal distance distribution between males and females.

Our results also show that wing size directly affects flight speed: the longer the wing, the faster the individual flies, and this is probably key to the dispersal mechanism of females. Studies performed on *Schistocerca gregaria* (Orthoptera: Acrididae) match our

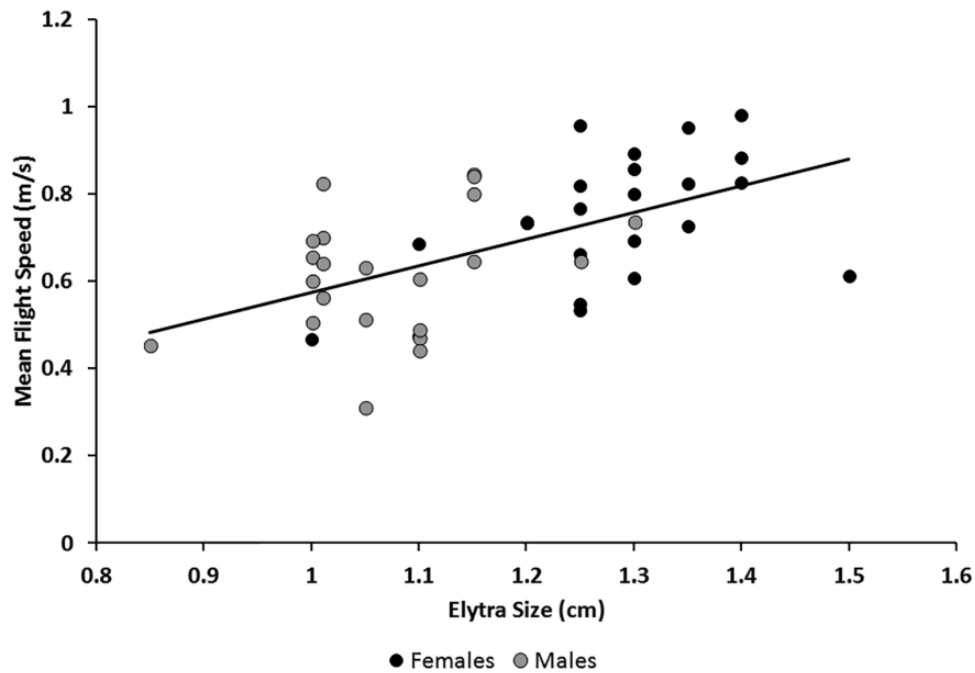


Fig. 2. Simple linear regression of elytra length (cm) and mean flight speed (m/s) of mated females and males of *A. rusticus*,  $n = 49$ ,  $R^2 = 0.34$ ,  $P < 0.0001$ .

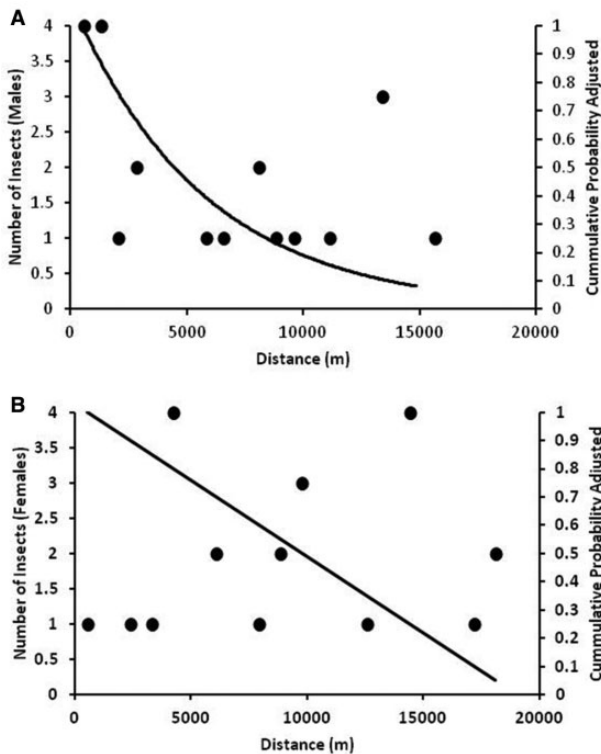


Fig. 3. Frequency distribution of the flight distance of mated males (A) and females (B) of *A. rusticus*. Solid line represents the adjusted probability distribution.

findings. In a series of experiments, Fischer and Kutsch (2000) found that, when wing areas were artificially reduced to the limit required to support body weight during free flight, the flight speed decreased in all the groups analyzed (Fischer and Kutsch 2000). The mechanism that relates wing length with flying speed is a basic biomechanics principle of insect flight. In insects, the aspect ratio of the wing

governs flight speed and maneuverability (Shyy et al. 2008). Aspect ratio is the ratio between the wingspan and the wing area, and can give an indication of the flight characteristics in insects. Agility and maneuverability improve with a lower aspect ratio. The induced drag that is caused by the lift decreases with higher aspect ratios (Shyy et al. 2008), i.e., longer wings will have less induced drag, increasing the flight speed with the same relative energy consumption. This matches what we found: the longer the wing, the faster the individual flies; and females were those with the longer wings.

No differences were observed in the percentage of weight loss between males and females, but it seems that the priority in this species in terms of energy consumption is reproduction, and secondly dispersal, as unmated individuals not only fly significantly less than mated individuals, but also do not spend the energy reserves they accumulate during the larval stage until mated. Insects usually show a trade-off between flight capabilities and other energy consumption activities such as reproduction. The energy cost of fuel biosynthesis for flight decreases the fitness of dispersing individuals.

In *A. rusticus*, as in other species of cerambycids, dispersal and reproduction depend on a single source of energy acquired during the larval stage (Coll and Yuval 2004). Resource allocation in dispersal or in reproduction in *A. rusticus* adults may be seen as the expenditure of capital resources accumulated during the larval stage. Species that invest the energy accumulated during the larval stages in reproduction are called “capital breeders” by Jervis et al. (2005). We consider that *A. rusticus* fits in this group, since females and males emerge sexually mature ready to copulate, as shown in this work. But they disperse only after copulation.

In a work on *Monochamus galloprovincialis*, David et al. (2015) extended the “capital” theory to dispersal in insects. Capital dispersers are thus insects like *A. rusticus*, which disperse using the energy obtained during their larval stage. Our results show that *A. rusticus* is a “capital disperser” only after being a “capital breeder,” as they consume the available energy reserves in dispersal only after copulation.

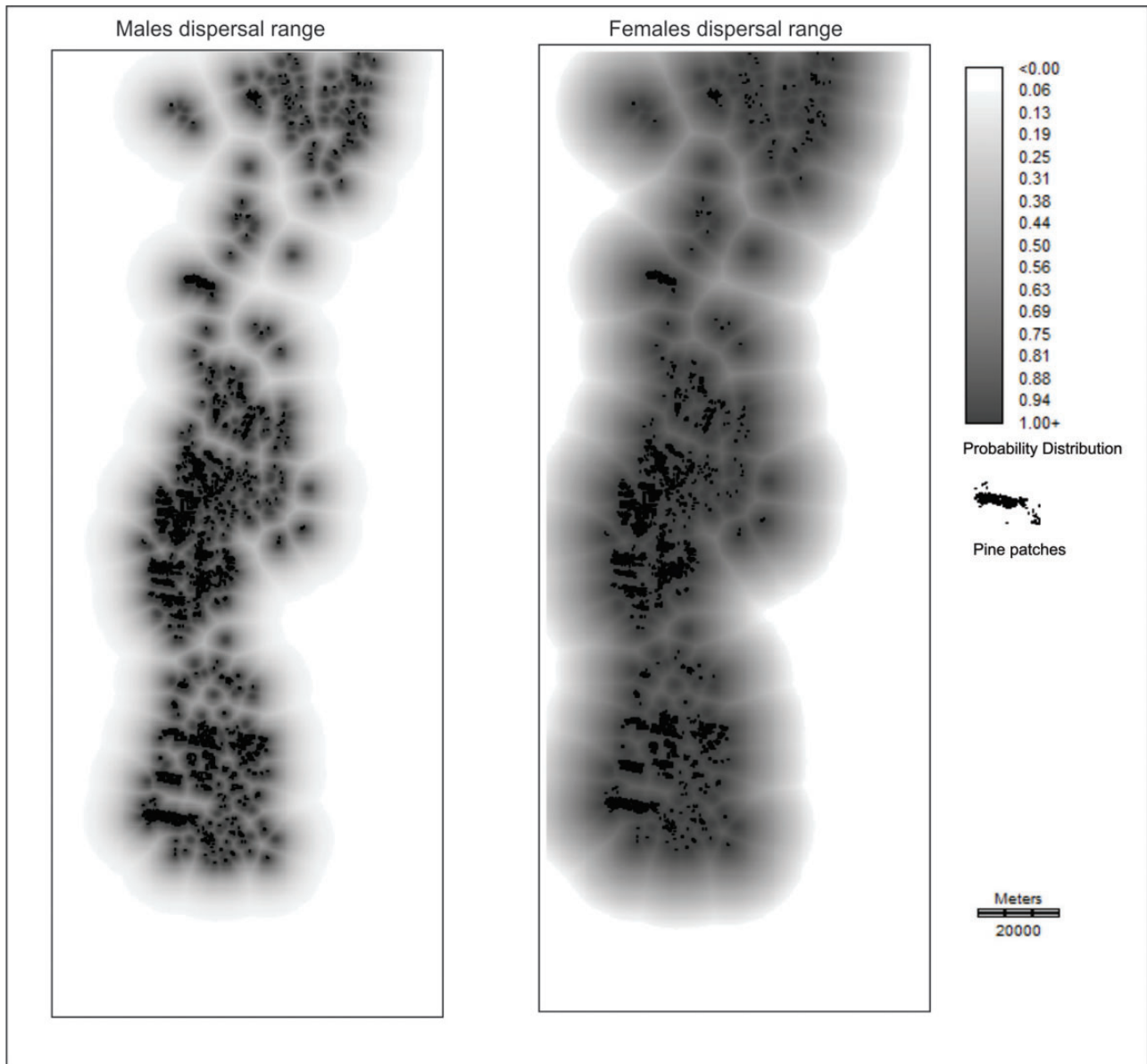


Fig. 4. Dispersal probability range of males and females of *A. rusticus* from each pine patch in the study area represented in Fig. 1.

In insects, mobility is very important, as it allows individuals to find resources, partners, or oviposition sites. In many cases, mobility enables species to persist in fragmented and altered environments, such as agricultural mosaics (Concepción et al. 2008), in which cases individuals must be able to reach habitat patches with the resources needed to survive (Dover and Settele 2009). Within the patch, mobility increases local population resilience to habitat disturbance, and is an indicator of the potential exchange of individuals between local populations (Kalarus et al. 2013). This is because individuals with greater mobility may potentially explore available resources within a habitat patch and can reach other patches in nearby habitats (Kalarus et al. 2013).

Wing length can be a secondary advantage for females, and a key feature for the colonization of new areas. Females of *A. rusticus* lay their eggs in clusters (~50 eggs per cluster) in crevices of the tree bark. They lay ~800 eggs, distributing their ovipositions between different trees (Kolk and Starzyk 1996). In the study forests, trees within a patch are between 2 and 5 m from each other. Considering

the flight speed of females observed in the flight mills, we estimated that they can visit 20% more trees than males in the same amount of time and, as they fly faster between trees, they are less exposed to predators during dispersal, which increases their reproductive success. They can also colonize more distant forests.

Most of the models employed to describe biological invasions explicitly track the densities of only one sex. A one-sex dispersal model is suitable only for asexual or hermaphroditic species, which includes most plants. The application of a one-sex model to dioecious species is complicated, basically because dispersal may be sex-biased, with males and females dispersing different distances, as in our case. Considering that, in most cases, it is in these far locations that population dynamics determine invasion speed, it is evident that a difference in the proportion of the sexes will affect the invasion speed via the Allee effect. It is predicted that, in an invader species, the Allee effect can cause a slower spread and a decrease in the probability of establishment (Hadjiavgousti and Ichtiaroglou 2004). There are many mechanisms that can give rise to the Allee effect.

The most frequent is that of mate shortage in sexually reproducing species (Boukal and Berec 2002). If the probability of mating decreases at decreasing densities, it is said that there is a “mate-finding Allee effect” (Gascoigne et al. 2009). If there is a decrease in male density because the dispersal range of the males is lower than that of females, then at that point the “mate-finding Allee effect” will be stronger. This can be overcome by dispersing species if mating occurs in those places where the abundance of males is optimal. In *Arhopalus rusticus*, this will be at the emergence site, prior to their dispersal from the logs.

In fluctuating environments, particularly when population size is large and dispersal cost is low, predispersal copulation will promote a female-biased dispersal pattern (Hirota 2004). In a very close species, *Arhopalus ferus*, females tend to emerge from the logs later than the males. Females emerge sexually mature and they mate almost immediately. Once they mate, females disperse while males generally remain in the emergence site (Hutcheson 1980). Something similar seems to occur in *A. rusticus*. Females do not disperse until they copulate and then they disperse almost twice the distance as males. Fertilized females can reap great fitness benefits from colonizing empty habitat patches and, as they are already fertilized, they are carrying not only their own genes but also the genes of their mating partners (Hirota 2004, 2005). Considering that dispersing females are carrying eggs, it is clear how the expansion of the species took place in the pine production area of Córdoba Province. Dispersal after copulation minimizes the risk of an Allee effect in the front line of expansion of the species and guarantees the colonization of new patches as females lay eggs as far as they can fly. Since its arrival in the central area of Argentina, *Arhopalus rusticus* has reached all of the pine patches in the area, proving to be a successful invader. This success appears to be due to its dispersal dynamic, increasing the chance of population establishment in new landscapes.

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