Survival and longevity in neotropical damselflies (Odonata, Polythoridae)

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Abstract
Survival and longevity in neotropical damselflies (Odonata, Polythoridae). Longevity among insect orders varies greatly, and has mainly been studied in insects in temperate biomes, where seasonality determines high synchronization of reproductive activities and limits lifespan. Most forest damselflies in tropical regions have low population densities and are almost never observed in copula. We hypothesized that selection will favour a high survival rate and hence high lifespan, allowing the animals to be ready for the occasional events that favour reproduction. We studied two neotropical damselflies, *Polythore mutata* and *P. derivata,* in Ecuador, using mark–recapture methods. We found that sex affected the rate of recapture, but daily survival rate was affected by sex only in one population. We found evidence that suggests stabilizing or directional selection on body size. The maximum lifespan was 54–63 days. We conclude that the survival rate of *Polythore* damselflies in tropical forests is comparable to that of similar damselflies in temperate zones.

Key words: Lifespan, Rainforest, Low density, Body size, Mark–recapture

Resumen
Supervivencia y longevidad de las libélulas del neotrópico (Odonata, Polythoridae). La longevidad, que entre los órdenes de insectos es muy variable, se ha estudiado principalmente en insectos de biomas templados, donde la estacionalidad determina una alta sincronización de las actividades reproductivas y limita la longevidad. La mayoría de las libélulas de las regiones tropicales vive en poblaciones con una densidad baja y casi nunca se observan en cópula. Nuestra hipótesis es que la selección favorecerá una alta tasa de supervivencia y, por lo tanto, una gran esperanza de vida, lo que permitiría que los animales estuvieran listos para los eventos ocasionales que favorecen la reproducción. Estudiamos dos libélulas neotropicales, *Polythore mutata* y *P. derivata*, en Ecuador, utilizando métodos de marcaje y recaptura. Constatamos que el sexo afectó a la tasa de recaptura, pero que solo afectó a la tasa de supervivencia diaria en una población. Hallamos indicios que sugieren la existencia de selección estabilizadora o direccional del tamaño del cuerpo. La longevidad máxima observada fue de 54–63 días. Concluimos que la tasa de supervivencia de las libélulas del género *Polythore* en los bosques tropicales es comparable a la de libélulas similares de las zonas templadas.

Palabras clave: Longevidad, Selva tropical, Baja densidad, Tamaño corporal, Marcaje y recaptura

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Introduction

Over the last decades, ecological research on natural populations of insects has accumulated a large dataset about survival and reproductive behaviour, allowing a good understanding of their reproductive strategies (Cornell and Hawkins, 1995). Longevity and fecundity among insect orders vary greatly, and recent evidence indicates that some insects live long enough to experience reproductive senescence (Sherratt et al., 2010). However while strong statistical evidence has been presented for senescence in vertebrate populations in the wild, we know little about the rate and shape of senescence in wild populations of insects. Most of this information comes from studies of insects in temperate biomes (Cordero–Rivera and Stoks, 2008), where seasonal regulation (Tauber and Tauber, 1976) and reproductive synchronization (Cordero Rivera and Andrés Abad, 1999) are clearly adaptive. Nevertheless, in tropical regions, where temperature remains almost constant, there are no cues to reproductive synchronization, except those derived from rain regimes (Wikelski et al., 2000). Odonates (damselflies and dragonflies) have been widely studied using mark–recapture methods in temperate regions (Cordero-Rivera and Stoks, 2008). For these reasons, studies of longevity of tropical damselflies are clearly needed (Cordero–Rivera and Stoks, 2008).

In tropical forests, some dragonflies are key species linking stream trophic networks to aerial networks, and are present at very low densities, particularly in South America. For instance, individuals of the family Calopterygidae can be found in their thousands in European streams but only a few scattered specimens can be found in the Amazon (for instance members of the genera *Hetaerina, Mnesarete* or *Ormenophlebia*) (Córdoba–Aguilar and Cordero–Rivera, 2005). In these tropical areas, reproductive activity is rarely observed. We hypothesized that animals must survive long periods to be able to reproduce when conditions are appropriate (e.g. Sanmartín–Villar and Cordero–Rivera, 2016).

Due to its particular individual and population traits, the family Polythoridae (Zygoptera) is a relevant model in ecology and evolution (Sánchez Herrera et al., 2015). A recent molecular phylogeny of this family suggests the existence of two clades, one grouping the species distributed across the Amazon basin and the other grouping species in the Andes (Sanchez Herrera et al., 2018). Most species of this genus possess sexual dimorphism, with males and females displaying different colour patterns. For example, the Amazonian species *Polythore mutata* (McLachlan, 1881) shows female colour polymorphism in addition to sexual dimorphism. The males and one phenotype of females (androchrome, similar colour to males) display a bright milky white band on the wings while the other phenotype of females (gynochrome, different colour to males) shows a bright orange band in the forewing and a violet band on the hindwing (Sanmartín–Villar and Cordero–Rivera, 2016). Beccaloni (1997) described several mimicry rings for the Ithomiinae butterflies in Jatun Sacha in Ecuador. This author suggested that *P. mutata* phenotypes converge in two of the seven mimicry rings he described for this geographic location. His work was mainly descriptive, but he also looked at the UV reflections which seemed to be consistent with the butterflies as well. Other researchers have anecdotally reported the similarities of the flight of *Polythore* damselflies with butterflies, and recent studies of the flight behaviour in the species *Polythore procera*, *Euthore fasciata* and *Gretta andromica* suggest that there is a mimicry signal among them (Outomuro et al., 2016a) wing shape, and flight style. The study species have wings with a subapical white patch, considered the aposematic signal, and a more apical black patch. The main predators are VS–birds, visually more sensitive to violet than to ultraviolet wavelengths.

Using multiple mark and recapture methods, we estimated recapture rates, survival probability and life expectancy of two geographically distant populations of *P. mutata* in Ecuador. Our hypothesis was that these animals have high survival (see above). We aimed to answer the following questions: 1) is the survival rate different between males and females?; 2) are both sexes recaptured with similar probabilities?; 3) for *P. mutata* females, is the survival probability of colour morphs the same?; and 4) does body length affect survival? Given the presence of a small population of *Polythore derivata* in one of the field sites, we also give a first analysis of survival in this species.

Material and methods

Field data collection

The field data collection and observations were conducted at two localities in Ecuador where *P. mutata* was previously recorded. The first location was the Tiputini Biological Station (TBS), at the border of Yasuni National Park (76.146041ºW, 0.635000ºS, Orellana province). We visited this location three times; from 4 to 12 December 2012, from 4 to 7 February 2013, and from 10 to 23 June 2013. However, at the third date, the density of *P. mutata* was extremely low and no marked individuals were resighted, which suggests that the time span of the study was appropriate for the expected lifespan of the species. A few individuals of *Polythore derivata* were observed during these sampling periods, but too few to be studied.

The second field site was the Jatun Sacha Biological Station (JSBS), near Tena (77.615677 ºW, 1.067593 ºS, Napo province), the same place visited by Beccaloni (1997). Here the density of *P. mutata* was higher than in Tiputini, and was accompanied by some *Polythore derivata* and isolated specimens of *Polythore concinna*. Field work was done during the dry season, between 30 October and 16 December 2014 (see Sanmartín–Villar and Cordero–Rivera, 2016, for further details).

In both localities, one to two observers walked over small streams and forest paths where the damselflies were found, for an average of 7 h per day. The animals

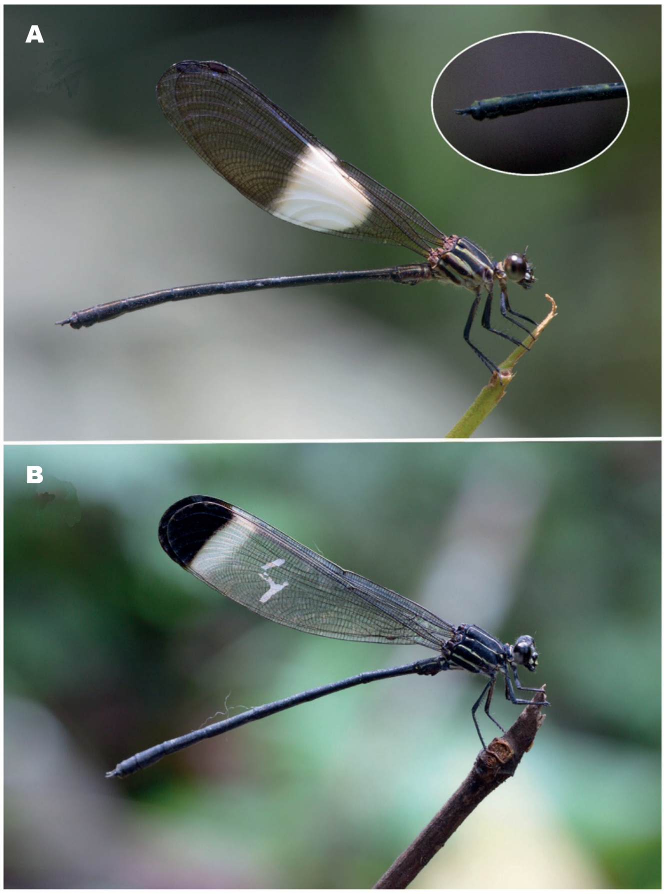

Fig. 1. A *P. mutata* male (A) from TBS and a *P. derivata* male (marked) (B) from JSBS. The insert in (A) shows the tip of the abdomen of a male *P. mutata* with algae growing, which is suggestive of old age. Pictures by ACR.

Fig. 1. Un macho de P. mutata *(A) de la estación biológica de Tiputini (TBS) y uno marcado de* P. derivata *(B) de la estación biológica de Jatun Sacha (JSBS). El círculo en (A) muestra el extremo del abdomen de un macho de* P. mutata *con algas, lo que sugiere que es de edad avanzada. Fotografias de ACR.*

were captured with an entomological net, measured with a calliper (body length to the nearest 0.1 mm, including anal appendages), marked with a white number in the wing (xylene–free white permanent marker; Pilot Super Color EF: www.pilotpen.com; fig. 1), photographed, and released. Re–sightings were carried out with the naked eye or using a Minox monocular, so that animals were only netted again if needed for specific reasons.

Mark and recapture analyses

To analyse mark–recapture histories we used the software Mark 8.1 (White and Burnham, 1999). Our analyses included sex and time (and their interaction) as factors to test for their effects on survival and recapture probabilities. Each population was analysed separately, because migration is extremely unlikely due to the high geographic distance between the populations (the linear distance is 167.2 km, estimated from GoogleEarth). We used the Information Theory Approach to rank models by their Akaike's Information Criterium (AIC), which is minimised in the models that are better supported by the data (Burnham and Anderson, 1998). However, this method does not allow to know whether the candidate models are good enough to explain the variability of the data. Therefore, we first tested the fit of the full time–dependent Cormack–Jolly–Seber model by groups using program Release. The model is defined by:

$$\text{Phi}(g{*}t)\ \text{p}(g{*}t)$$

where *Phi* and *p* represent the recapture and survival probability, *g* is sex and *t* is time.

In the case of TBS, this model showed good adjustment for males of *P. mutata* (Goodness of fit results (Test 2 + Test 3): $\chi^2_{18} = 15.71$, $p = 0.613$), but due to the low recapture rate of females, this

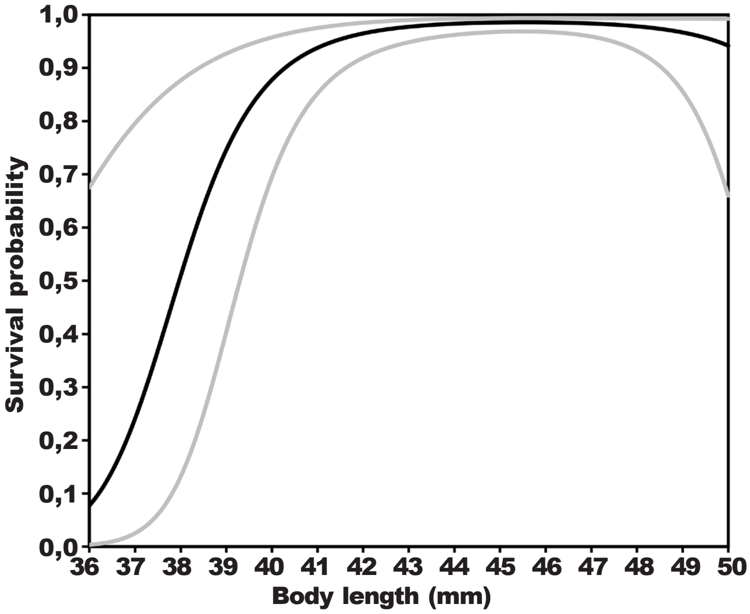

Fig. 2. The relationship between body length and survival probability of *P. mutata* at Tiputini (sexes combined). Note that the estimates suggest stabilizing selection. Grey lines indicate 95% confidence intervals.

Fig. 2. Relación entre la longitud corporal y la tasa de supervivencia de P. mutata *en Tiputini (sexos combinados). Nótese que las estimaciones sugieren la existencia de una selección estabilizadora. Las líneas grises indican el intervalo de confianza del 95%.*

test could not be calculated. The adjustment was clear in the case of *P. mutata* from JSBS (Test 2 + 3 by groups: males χ^2_{52} = 22.73, p = 1; females χ^2_{27} = 8.21, p = 1). For *P. derivata* at JSBS, only males were recaptured, and again the saturated model showed good adjustment (Test 2 + 3: males χ^2_{14} = 9.10, p = 0.825). In JSBS we ran an analysis of *P. mutata* females only to test for differences between morphs. The saturated model was also appropriate (Test 2 + 3 by morph: androchrome χ^2_7 = 0.00, p = 1; gynochrome χ^2_7 = 9.45, p = 0.977).

The second step was to estimate the variance inflation parameter (c–hat) by two methods. We divided the c–hat obtained from model Phi(g*t) p(g*t) by the mean c–hat of the bootstrap simulations in Mark. With this method we always obtained c–hat = 1. The second method divided the deviance of the saturated model by the mean deviance of the bootstrap procedure. Values ranged between 0.98 and 1.27. No correction was done when c–hat was lower than one, but otherwise c–hat estimates were used to adjust parameter estimates and standard errors.

In the next step, we ran models without individual covariates, to select the most supported model, as the one that minimizes Quasi Akaike's Information Criterion (QAIC). Once these models were identified, body length was included as an individual covariate, both as linear and quadratic terms. When there was statistical support for more than one model, estimates of parameters were obtained by model averaging using Mark software and are shown as average probability ± SE. We estimated the expected longevity using the formula of Cook et al. (1967):

$$\text{Longevity} = 1 / \log_e(\text{survival})$$

Results

Overall, population density of both *Polythore* species was low. At TBS, we marked 21 males and 13 females of *P. mutata* in December 2012 and 16 males and 5 females in February 2013, and recaptured four males and one female from 2012. No marked animals were found in June 2013. At JSBS we marked 76 males and 35 females of *P. mutata*, 19 males and five females of *P. derivata* and three males and one female of *P. concinna*. This last species is not analysed here due to the lack of recaptures. Female polymorphism was detected in both populations of *P. mutata.* In TBS we only observed one androchrome female in the first period (that could not be marked) and marked another androchrome female in the second sampling period, with an overall frequency of 5.6% androchromes (1 out of 18 females), while at JSBS, androchromes were 40% (14 out of 35). No female polymorphism was detected in *P. derivata* (see also Sanmartín–Villar and Cordero–Rivera, 2016).

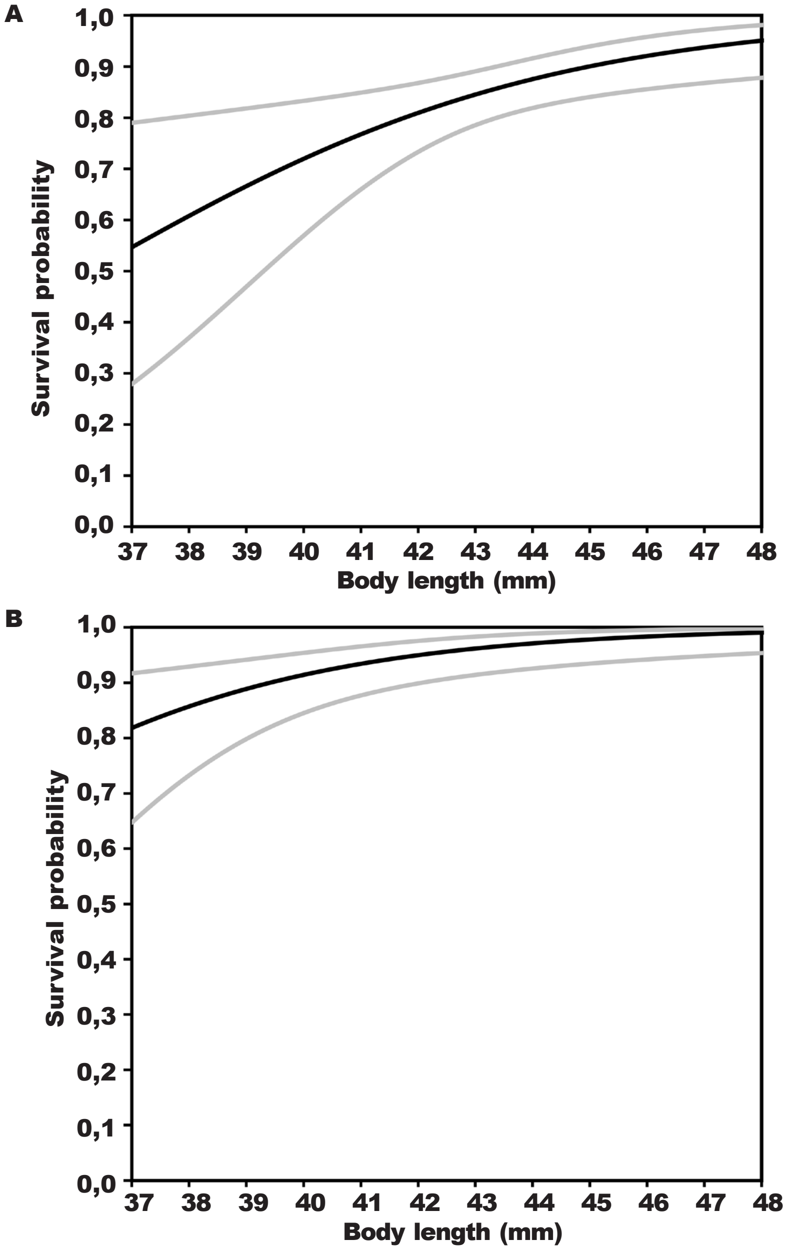

Fig. 3. The relationship between body length and survival probability of *P. mutata* at Jatun Sacha. There was positive directional selection in both sexes: A, males; B, females. (Grey lines indicate 95% confidence intervals).

Fig. 3. Relación entre la longitud corporal y la probabilidad de supervivencia de P. mutata *en Jatun Sacha. Hubo selección direccional positiva en ambos sexos: A, machos; B, hembras. (Las líneas grises indican el intervalo de confianza del 95 %).*

Considering both sexes, at TBS model selection by AIC_c indicates that the best model is {Phi(.) p(g)}, which means similar survival for males and females and a different recapture rate by sex. The inclusion of body size as a covariate (table 1s) indicates that survival is affected by body size, and that the best model includes the quadratic term, suggesting stabilizing selection (fig. 2). Given that the best model has a $\Delta\text{AIC}_c = 3.8$ (table 1s), no model averaging was needed, and we estimated daily survival rate from the best model as 0.974 ± 0.011 (expected longevity 38 days) and recapture rates 0.391 ± 0.047 for males and 0.081 ± 0.041 for females.

At JSBS, the model selected by AIC$_c$ is {Phi(g) p(.)}, the opposite to the previous case (table 2s), indicating higher survival rates for females, while the recapture rate was similar for males and females. Including body length as a linear covariate improved the fit of this model, but the quadratic term diminished fit. Therefore, our data for JSBS suggest a positive directional selection for larger body length (fig. 3) in both sexes. Using model averaging, the daily survival rate was estimated as 0.821 ± 0.032 for males (expected longevity 5.1 days) and 0.953 ± 0.019 for females (20.8 days), with a common recapture rate of 0.200 ± 0.024.

The analysis of recapture histories of the JSBS polymorphic females of *P. mutata* was limited by the low number of specimens found. On some dates, only one morph was found, and therefore interactions morph*time could not be calculated at these dates, and models including these interactions were excluded. The best model, as selected by AIC$_c$, was {Phi(.) p(g)}, and the second {Phi(g) p(g)}, and both were much more supported than the next models (ΔAIC$_c$ > 4.3; table 2s). Using model averaging, we found the daily survival rate was estimated as 0.927 ± 0.034 (expected longevity of 13.2 days) for androchromes and 0.943 ± 0.021 (longevity 17.0 days) for gynochromes, and recapture rates 0.088 ± 0.038 for androchromes and 0.247 ± 0.044 for gynochromes. Recapture rates were clearly different between morphs, and there is some evidence for higher survival by gynochromes.

Finally, we analysed the recapture histories of males of *P. derivata* from JSBS (no females were recaptured). In this case, given the small sample size (N = 16 males) we could not use covariates. The best model was the simplest one, with constant survival and recapture probabilities ({Phi(.) p(.)} indicating a survival rate of 0.962 ± 0.018 and a recapture rate of 0.241 ± 0.048, with an expected longevity of 25.6 days.

Some observations might suggest higher lifespan than our estimates. For instance, some individuals showed algae and even bryophytes over the body surface (fig. 1A) at TBS. In addition, five individuals marked in December at TBS, were found alive in February, with a lifespan between 54 and 63 days. The proportion of animals with algae on the abdomen was 15.6% in December and 38.5% in February, when most of the specimens were clearly older. Three of the animals surviving from December to February showed algae on the abdomen, but none of these had algae present when first marked.

Discussion

We found that *Polythore mutata* and *P. derivata* damselflies have a high survival rate and low recapture probabilities, particularly in females. Mark–recapture studies provide information based on the subset of animals that are recaptured, and therefore the estimates are valid only if temporal emigration does not occur, and when emigration is permanent, this cannot be disentangled from mortality (Lebreton et al., 1992). Examination of trade–offs between reproduction and survival rely on individually marked animals, for which the exact time of death is most often unknown, because marked individuals cannot be followed closely through time. These limitations are to be taken into account when interpreting our results.

For other Polythoridae, like *Polythore procera,* estimates of survival are ~0.97 (Sánchez–Herrera and Realpe, 2010), and ~0.40 to 1, depending on the population for *P. gigantea* (Altamiranda–Saavedra and Ortega, 2012), which are similar to our estimates. The analysis of recapture rates suggests that females were less often resighted at TBS, whereas at JSBS, about 20% of individuals were resighted, irrespective of sex. In contrast, recapture probabilities for the Andean species previously studied yielded higher estimates (Sánchez–Herrera and Realpe, 2010; Altamiranda–Saavedra and Ortega, 2012) than for our Amazonian species. Andean species of *Polythore* showed higher density of individuals overall than those in the Amazonian field sites we evaluated here. The preferred habitat of *Polythore* (i.e. rocky waterfalls, small creeks) is not common in the Amazon in comparison with the Andean foothills. In particular, the difference between the TBS and JSBS may be explained by the fact that observations at TBS were mainly done near the stream, where males showed high site fidelity and territorial behaviour, whereas at JSBS the topography allowed a more extensive examination of the areas around the streams and in the forest. In fact, some females were found feeding at the same sunspots in the forest for several days. Therefore, our data suggest that the lower recapture rate of female damselflies (Cordero–Rivera and Stoks, 2008) is due to females remaining at larger distances from the water. This behaviour was also observed for the Andean *P. procera,* where the females seem to remain at highly dense forest areas, while males remained near the open stream area (Sánchez–Herrera et al., 2010).

At TBS, we found that survival probabilities were not affected by sex, while at JSBS they were higher for females, and were in the interval 0.821–0.974. These survival values translate into longevities of five to 38 days, similar to the maximum longevity observed in other damselflies from temperate regions (Cordero–Rivera and Stoks, 2008). Therefore, we did not find evidence of long pre–reproductive periods or high survival, contrary to our expectations. However, the presence of algae and liverworts growing on the abdomen and wings of some specimens (fig. 1A) suggests that they have lived in the humid forest for months (Lücking et al., 2010) because these algae cannot be acquired during the larval stage (the cuticle changes after metamorphosis) and because liverworts have a long life cycle (Lücking et al., 2010). Our estimates of maximum lifespan are thus likely below the real values. To test this hypothesis, future studies should include longer periods of fieldwork to maximize the probability of detecting a particularly high lifespan. Records of algae growing on rainforest odonates are very rare and have been interpreted as indicators of old age (e.g. Fincke and Hadrys, 2001). Algae were also found in other Ecuatorian species such as *Metaleptobasis sp*, *Argia oculata*, *Heteragrion cooki*, *Hetaerina fuscoguttata*, and *Uracis imbuta* (ACR, ISV and ART personal observations, 2014, 2016), and some odonates in rainforests in Yunnan (China, ACR, pers. obs. 2016). However, even the longest–living specimens in our samples were unlikely to live for more than two months. Higher longevity could also be the result of the low activity levels of *Polythore* individuals, which remained perched immobile almost all the time (see Sanmartín–Villar and Cordero–Rivera, 2016), but nevertheless showed nervous behaviour (they quickly escaped when a human approached) which is probably an efficient antipredator strategy. Finally, their possible mimicry to poisonous butterflies could also contribute to high survival (Beccaloni, 1997). This topic is worth exploring in future field experiments.

Female colour polymorphism for *P. mutata* was also evidenced in the TBS population, which constitutes the first evidence of this polymorphism out of JSBS. However, we only saw two andromorphs throughout the whole sampling dates for TBS. Therefore, even though there are polymorphic individuals in different populations, the selective forces maintaining the polymorphism might differ depending on the geographic location. Beccaloni's (1997) suggestion of convergence of these morphs within two Ithomiinae mimicry rings for JSBS could play a role as a selective force potentially maintaining higher survival probabilities for *P. mutata.* Our results show little evidence for an effect of female colour morph on survival rate in females of *P. mutata*. These results are to be taking with caution because the number of females resighted was low, but they agree with previous work on other polymorphic damselflies (e.g. Andrés and Cordero–Rivera, 2001) that suggest no effect of female colour morphs on survival. Few studies however have applied the modern techniques of capture–recapture analysis (Lebreton et al., 1992) to polymorphic damselflies, and further research is clearly needed on this topic. The conspicuousness of the wings in male and androchrome females of *P. mutata* might be higher than that in gynochrome females, at least for predators that perceive the UV range (Bick and Bick, 1965). In addition, no androchrome females were observed near the streams where males concentrated, even in JSBS, where androchromes were common. This suggests the two female phenotypes have different reproductive strategies, a common phenomenon in other damselflies (Van Gossum et al., 2008). Future experiments are needed to decipher the significance of this polymorphism.

We found that adding body length as a covariate in the mark–recapture analysis increases the fit of the models. At TBS, we found evidence that suggests stabilizing selection for body size, whereas at JSBS larger body length was apparently under positive selection. In fact, the average size of males at JSBS (42.9 ± 0.27, SE, N = 72) was smaller than the size of males at TBS (43.9 ± 0.45, N = 34; $t_{104} = -2.109$, $p = 0.037$). A recent review of body size evolution in the Odonata found a consistent trend of positive selection for larger size, but at the same time no evidence for an increase in body size over evolutionary time. The authors suggested that this lack of concordance is due to the trade–off between larger body size as adults and longer larval life (Waller and Svensson, 2017). Survivorship seems more related to body size for JSBS males than for females (compare the slopes in fig. 3). This could be explained by the territorial behaviour and the positive relationship between body size and reproductive success in males and the lack of relationship for this trait and fitness in many females (Serrano–Meneses et al., 2007; Sanmartín–Villar and Cordero–Rivera, 2016). In the case of TBS our results suggest stabilizing selection (fig. 2). It is possible that small males were excluded from the best areas by the aggressive behaviour of larger males. However, survivorship also decreased in the largest body sizes. This might be due to the associated cost of large bodies (e.g. maintenance, decrease of manoeuvrability, conspicuousness towards predators) or/and the different directions of natural and sexual selection in those traits (Outomuro et al., 2016b). Our results indicate that survival can or cannot be positively related to larger body size in these damselflies, possibly depending on local ecological conditions. A previous study of another forest damselfly found that in a sunny stream, body size was negatively correlated with survival, but in a shaded environment it was not (Rivas–Torres et al., 2017). Another possibility is that survival may show interannual variation, a suggestion that also merits further study. It seems likely that contrasting selective regimes between natural and sexual selection in adults, between larvae and adults (Waller and Svensson, 2017), and between years and localities contributes to the stasis observed on body size over time.

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Table 1s. Results of model selection for *P. mutata* at TBS. Survival rate is denoted by Phi and recapture probability by p. The group is the sex (g) and time variation is indicated by t. The best models include body length as covariate (body).

Tabla 1s. Resultados de la selección de modelos para P. mutata *en la estación biológica de Tiputini (TBS). La tasa de supervivencia se indica como Phi y la probabilidad de recaptura, como p. El grupo es el sex (g) y la variación temporal se indica como t. Los mejores modelos incluyen la longitud corporal como covariable (body).*

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(body+body2) p(g)}	263.923	0.000	0.787	1.000	5	253.292
{Phi(body) p(g)}	267.735	3.812	0.117	0.149	4	259.319
{Phi(.) p(g)}	269.092	5.169	0.059	0.075	3	262.845
{Phi(g) p(g)}	270.343	6.419	0.032	0.040	4	261.926
{Phi(.) p(g*t)}	275.353	11.429	0.003	0.003	23	215.015
{Phi(.) p(t)}	277.137	13.213	0.001	0.001	13	246.953
{Phi(g) p(t)}	278.053	14.129	0.001	0.001	14	245.169
{Phi(g) p(g*t)}	278.803	14.880	0.000	0.001	24	215.014
{Phi(t) p(g)}	281.304	17.381	0.000	0.000	14	248.421
{Phi(t) p(t)}	293.578	29.654	0	0	24	229.788
{Phi(g) p(.)}	293.850	29.927	0	0	3	287.603
{Phi(.) p(.)}	294.091	30.168	0	0	2	289.969
{Phi(t) p(g*t)}	300.979	37.056	0	0	34	196.919
{Phi(t) p(.)}	301.301	37.378	0	0	13	271.117
{Phi(g*t) p(g)}	308.796	44.872	0	0	24	245.006
{Phi(g*t) p(.)}	321.948	58.025	0	0	23	261.611
{Phi(g*t) p(t)}	324.809	60.885	0	0	34	220.748
{Phi(g*t) p(g*t)}	330.635	66.711	0	0	40	195.968

Table 2s. Results of model selection for *P. mutata* at JSBS. Survival rate is denoted by Phi and recapture probability by p. The group is sex (g) and time variation is indicated by t. The best models include body length as covariate (body).

Tabla 2s. Resultados de la selección de modelos para P. mutata *en la estación biológica de Jatun Sacha (JSBS). La tasa de supervivencia se indica como Phi y la probabilidad de recaptura, como p. El grupo es el sex (g) y la variación temporal se indica como t. Los mejores modelos incluyen la longitud corporal como covariable (body).*

Model	QAICc	ΔQAICc	AICc Weights	Model Likelihood	Num. Par	QDeviance
{Phi(g+body) p(.)}–not standardized}	534.124	0.000	0.748	1.000	4	525.917
{Phi(g+body+body2) p(.)}–not standardized}	536.691	2.567	0.207	0.277	6	524.253
{Phi(g) p(.)}	541.009	6.886	0.024	0.032	3	534.886
{Phi(g) p(g)}	542.985	8.861	0.009	0.012	4	534.779
{Phi(.) p(.)}	543.619	9.495	0.006	0.009	2	539.558
{Phi(g+body) p(.)}–standardized}	544.878	10.754	0.003	0.005	4	536.672
{Phi(.) p(g)}	545.573	11.449	0.002	0.003	3	539.450
{Phi(g) p(t)}	595.728	61.604	0	0	41	491.791
{Phi(.) p(t)}	596.340	62.217	0	0	40	495.581
{Phi(t) p(.)}	610.211	76.087	0	0	39	512.588
{Phi(t) p(g)}	613.337	79.213	0	0	40	512.578
{Phi(.) p(g*t)}	710.521	176.398	0	0	76	462.587
{Phi(g) p(g*t)}	711.179	177.055	0	0	77	457.906
{Phi(t) p(t)}	712.677	178.554	0	0	74	475.161
{Phi(g*t) p(.)}	724.970	190.846	0	0	73	492.538
{Phi(g*t) p(g)}	730.035	195.912	0	0	74	492.519
{Phi(g*t) p(t)}	924.270	390.146	0	0	107	456.292
{Phi(t) p(g*t)}	938.379	404.256	0	0	110	440.879
{Phi(g*t) p(g*t)}	1319.746	785.622	0	0	137	425.877