DR CAROLINE DONG (Orcid ID : 0000-0003-3352-4006)

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RUNNING TITLE: Parental effects on hybrid fitness

TITLE: Maternal reproductive output and F1 hybrid fitness may influence contact zone dynamics

AUTHORS: Caroline M. Dong[1*], Katrina J. Rankin[2], Claire A. McLean[3], Devi Stuart-Fox[4]

[1]School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
Sciences Department, Museums Victoria, Carlton Gardens, Victoria, Australia
Present address: Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana, United States
Email: cdong1@tulane.edu
Twitter: colorfulagamids
*Author for correspondence

[2]School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
Email: katrina.rankin@unimelb.edu.au
Twitter: kjrankin88

[3]School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
Sciences Department, Museums Victoria, Carlton Gardens, Victoria, Australia
Email: cmclean@museum.vic.gov.au

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Twitter: Claire_A_McLean

[4]School of BioSciences, The University of Melbourne, Parkville, Victoria, Australia
Email: d.stuart-fox@unimelb.edu.au

Abstract

The outcome of secondary contact between divergent lineages or species may be influenced by both the reproductive traits of parental species and the fitness of offspring; however, their relative contributions have rarely been evaluated, particularly in longer lived vertebrate species. We performed pure and reciprocal laboratory crosses between *Ctenophorus decresii* (tawny dragon) and *C. modestus* (swift dragon) to examine how parental reproductive traits and ecologically-relevant offspring fitness traits may explain contact zone dynamics in the wild. The two species meet in a contact zone of post-F1 hybrids with asymmetric backcrossing and predominantly *C. modestus* mtDNA haplotypes. We found no evidence for reduced parental fecundity or offspring fitness for F1 hybrid crosses. However, maternal reproductive strategy differed between species, irrespective of the species of their mate. *Ctenophorus modestus* females had higher fecundity and produced more and larger clutches with lower embryonic mortality. Parental lineage also influenced sex ratios and offspring traits, with *C. modestus* ♀ × *C. decresii* ♂ hybrids exhibiting higher trait values for more fitness measures (growth rate, sprint speed, bite force) than offspring from all other pairings. Together, these patterns are consistent with the prevalence of *C. modestus* mtDNA in the contact zone, and asymmetric backcrossing likely reflects fitness effects that manifest in the F2 generation. Our results highlight how parental species can influence multiple offspring traits in different ways, which together may combine to influence offspring fitness and shape contact zone dynamics.

Keywords: captive-breeding, *Ctenophorus decresii*, *Ctenophorus modestus*, hybridisation, life history, lizard, reinforcement, reproductive isolation

Introduction

Hybridisation is an important evolutionary process that can influence the trajectory or persistence of one or both parental species. Although hybridisation occurs across a wide range of spatial and temporal contexts, there are three possible distinct outcomes: a stable equilibrium (i.e.

tension zone), the breakdown of barriers due to gene flow and recombination, or the strengthening of barriers driving further divergence (reviewed in Abbott et al. 2013). During secondary contact, the viability and fertility of first generation (F1) hybrids in particular may determine the long-term consequences of hybridisation by precluding, reducing or facilitating gene flow in one or either direction (Arnold et al., 2012). Numerous studies have investigated genetic and phenotypic patterns across naturally occurring contact zones but few have concurrently used laboratory studies of parental reproductive output and hybrid fitness to aid in interpreting patterns observed (but see MacGregor et al., 2017; Orr, 1996; Peterson et al., 2005; Rank et al., 2020; Scribner, 1993; While et al., 2015). An interplay of intrinsic and extrinsic factors governs F1 fitness, and laboratory studies (e.g. captive breeding) may enable stronger inferences about the nature of reproductive isolating barriers. For example, the absence of post-F1s across a beetle hybrid zone (*Chrysochus auratus* and *C. cobaltinus*), in conjunction with the reduced fertility of F1 hybrid females in a laboratory setting, suggested that the hybrid zone represented a tension zone between these species (Peterson et al., 2005).

Intrinsic low hybrid fitness is generally attributed to Dobzhansky-Muller incompatibilities (DMIs; Dobzhansky, 1937; Muller, 1942) between biparentally inherited autosomal loci (nuclear-nuclear). Postzygotic barriers are expected to select for the formation of prezygotic barriers to avoid maladaptive hybridisation, thereby promoting speciation (Dobzhansky 1937; reviewed in Butlin 1987; Howard 1993; Noor 1999; Turelli et al. 2001; Servedio and Noor 2003; Coyne and Orr 2004; Servedio 2004; Ortiz-Barrientos et al. 2009; Abbott et al. 2013; Pfennig 2016). This process of reinforcement following secondary contact is thought to complete speciation initiated in allopatry (Hoskin et al., 2005). Conversely, increased hybrid fitness may result in hybrids outcompeting parental lineages (Huxel, 1999; Rhymer & Simberloff, 1996; Rosenfield et al., 2004; Taylor et al., 2006), the formation of a stable hybrid zone when hybrids only have higher fitness in the distinct habitat of the contact zone (Nosil et al., 2009) or in tension zones (Barton & Hewitt, 1985), or hybrid speciation (reviewed in Mallet 2007). Fitness disparities between reciprocal hybrids may arise from DMIs involving sex chromosomes or cytoplasmic factors (e.g. mitochondria, chloroplasts; Arntzen et al., 2009; Bolnick et al., 2008; Bolnick & Near, 2005; Rank et al., 2020; Tiffin et al., 2001), and may also be shaped by exogenous selection (Campbell & Waser, 2001; Kimball et al., 2008; Muir et al., 2015; Wesselingh et al., 2019). To distinguish these possibilities, laboratory crosses to assess differences in both parental fecundity and hybrid fitness are essential.

Here, we investigate differences in parental reproductive output and the fitness of F1 hybrids produced from captive-breeding between *Ctenophorus decresii* (tawny dragon; Duméril & Bibron, 1837) and *C. modestus* (swift dragon; Ahl, 1926), which were previously regarded as divergent lineages of *C. decresii sensu lato* (Dong et al., 2021). *Ctenophorus decresii sensu stricto* (previously southern lineage *C. decresii*) and *C. modestus* (previously northern lineage *C. decresii*) differ in male coloration and meet naturally in a zone of secondary contact (Figure 1). *Ctenophorus modestus* males are polymorphic with four co-occurring throat colour morphs (orange, yellow, yellow with orange centre, and grey), whereas *C. decresii* males are monomorphic with blue throats that reflect ultraviolet (UV) wavelengths (McLean et al., 2014; Teasdale et al., 2013). Secondary contact between populations or lineages that differ in colour morphs is predicted to generate genetic incompatibilities due to the role of colour signals in reproductive isolation (Boughman, 2001; Jiggins et al., 2001; Mavárez et al., 2006; Sætre et al., 1997; Seehausen et al., 2008) and the genetic architecture of colour polymorphism (Sinervo & Svensson, 2002). We recently showed that the polymorphic throat coloration is the target of selection during incipient speciation between *C. decresii* and *C. modestus* (Dong et al., 2019), consistent with the view that colour polymorphism can promote speciation (Corl, Davis, Kuchta, & Sinervo, 2010; Forsman, Ahnesjö, Caesar, & Karlsson, 2008; Gray & McKinnon, 2007; Hugall & Stuart-Fox, 2012; McLean & Stuart-Fox, 2014; West-Eberhard, 1986). The contact zone represents a hybrid swarm and there is evidence of intrinsic incompatibilities, with admixed individuals primarily having *C. modestus* mtDNA haplotypes and genomic patterns indicating restricted backcrossing to *C. decresii* (Dong et al., 2019; McLean et al., 2014). Further, captive behavioural trials indicate incomplete and asymmetric behavioural barriers to mating, with stronger barriers between *C. decresii* males and *C. modestus* females than the reciprocal combination driven by both male and female mate preferences (McLean et al., 2020). Specifically, *C. decresii* males displayed a preference for conspecific individuals and *C. modestus* females were generally more choosy (displayed more rejection behaviours), whereas *C. modestus* males and *C. decresii* females did not discriminate between con- and heterospecific individuals.

In order to assess the nature and extent of reproductive isolating barriers, we conducted a captive-breeding experiment to produce all pairwise combinations of crosses using genetically pure parental populations from either end of the contact zone. We compared parental reproductive life history traits and the viability and fitness of F1 hybrids relative to that of pure offspring. We measured offspring survival, growth rate, maximum bite force, and maximum sprint speed as proxies of competitive ability and fitness, as these traits strongly correlate with ecologically relevant tasks and are known to be the target of selection (reviewed in Irschick et al., 2007; Wainwright, 2007). Based on the structure of the contact zone, we predicted that F1 hybrids would have lower fitness than pure crosses, due to the low prevalence of F1 hybrids and near absence of individuals backcrossed to *C. decresii*. Furthermore, given the prevalence of *C. modestus* mtDNA haplotypes in the contact zone, we predicted greater reproductive output by *C. modestus* mothers and/or that hybrids with *C. decresii* mtDNA haplotypes (i.e. *C. decresii* mother) may suffer from reduced viability and/or fitness. We discuss the implications of our results for inferring the consequences of secondary contact and trajectories of parental populations.

Materials and Methods

Animals

Ctenophorus decresii and *C. modestus* are small (snout-vent-length [SVL] ≤ 90 mm) rock-dwelling agamid lizards endemic to South Australia. We captured individuals from the wild in 2015 and 2016 (September – November) using a standard lassoing protocol or by hand. This included 18 adult female and 21 adult male *C. modestus* from the vicinity of Caroona Creek Conservation Park (longitude: 139.103°, latitude: −33.443°, ca. 130 km north of the contact zone centre) and 17 adult female and 18 adult male *C. decresii* from the vicinity of Palmer (longitude: 139.159°, latitude: -34.851°, ca. 30 km south of the contact zone centre) in South Australia (Figure 1). These populations represent the nearest pure parental populations to the contact zone. Lizards were housed individually in an indoor facility at The University of Melbourne, Melbourne, Australia, in 55 cm × 34 cm × 38 cm (length [L] × width [W] × depth [D]) opaque plastic enclosures containing a layer of sand and two stacked ceramic tiles for shelter and basking. Lizards were fed live crickets and mealworms *ad libitum* three times per week and misted with water for hydration. The room was maintained at temperature and lighting regimes that reflected natural seasonal variation, with appropriate UV lighting (Outback Max 10.0 UVA/UVB). Heat lamps were provided in each enclosure to generate a thermal gradient and allow animals to attain their preferred body temperature (36°C; Gibbons, 1977; Walker, unpublished data).

Captive breeding

Our objective was to produce pure offspring (*C. modestus* ♀ × *C. modestus* ♂, *C. decresii* ♀ × *C. decresii* ♂) and reciprocal cross hybrids (*C. modestus* ♀ × *C. decresii* ♂, *C. decresii* ♀ × *C. modestus* ♂). The sexes of each species were equally partitioned into two groups (when possible), all individuals of each group were paired with either a same-species mate or opposite-species mate to produce a clutch of eggs, and this was reversed in the next reproductive cycle for up to three cycles within the breeding season. If a female did not become visibly gravid after two weeks, she was paired with an alternative equivalent-species male to increase the likelihood of copulation in each cycle. Females mate again after oviposition; therefore, for the next reproductive cycle, one to two days following oviposition, females were housed with a male of the opposite species from the previous mate. Males of each species followed the same partitioning and pairing procedure such that they encountered alternating species females. Breeding trials were conducted in October – December 2017, during their natural breeding season.

Nest boxes were provided in the form of 17 cm × 13 cm × 15 cm (L × W × D) clear plastic enclosed containers with a 3.5 cm circular entrance in a lower corner and damp 50:50 sand:peat moss mixture sloped upwards to the top of the box. For lizards, most females will bury their clutches when provided with a suitable nesting area but inexperienced individuals may lay clutches in the open (Sanger et al., 2008). To account for clutches laid in the open, where they are vulnerable to desiccation, gravid females were checked for evidence of oviposition up to five times daily. Eggs were collected following oviposition (typically within one hour) and individually weighed to the nearest 0.01 g using a digital balance. Eggs were incubated in sealed plastic containers filled two-thirds with moist vermiculite (volume ratio 5:1 vermiculite:water) and incubated at 28°C (± 0.12°C) until hatching. This incubation temperature was chosen for a 50:50 sex ratio (Rankin et al., 2016).

Measuring parental reproductive traits

Indicators of female reproductive output were: fecundity, clutch size, embryonic mortality, egg mass at oviposition, and offspring mass at hatching. Female fecundity was measured as total reproductive output across the breeding season (i.e. total mass of eggs produced across clutches). Embryonic mortality was scored based on the presence of calcification of the egg shell and/or failure to hatch (Olsson & Shine, 1997). Following the breeding season, we recorded male testes mass as this trait may be under sexual selection in lizards (Olsson & Madsen, 1998). Males were humanely killed, and testes were dissected and weighed to the nearest 0.01 g on a digital balance.

Offspring rearing conditions

Experimental crosses resulted in a total of 53 clutches comprising 259 eggs of which 211 were able to be incubated (i.e. laid in nest boxes or found before they had desiccated). Of these, 176 viable offspring hatched: 69 out of 73 pure *C. modestus* (94.5%), 14 out of 22 pure *C. decresii* (63.6%), 61 out of 67 hybrids sired by *C. decresii* males (91.0%), 32 out of 41 hybrids sired by *C. modestus* males (78.1%). Offspring were raised for a minimum of six months under laboratory conditions and housed individually in 30 cm × 20 cm × 10 cm (L × W × D) plastic enclosures with fly screen lids. Each enclosure contained two stacked ceramic tiles to provide shelter with paper substrate and a water dish. Ambient temperature was maintained at 24°C, UV lighting was provided, and a heat lamp was positioned at one end of the enclosure for a basking temperature of 31°C. Hatchlings were fed pinhead crickets and fruit flies (*Drosophila*) *ad libitum* twice daily and misted with water. At three months post-hatching, their diet was changed to small crickets *ad libitum* daily, supplemented with mealworms.

Measuring offspring fitness

We recorded offspring SVL (mm) with digital callipers and mass (g) with a digital balance, both to the nearest 0.1, immediately post-hatching and then at weekly intervals for 24 weeks. We used SVL as a measure of growth rate rather than mass because it does not vary with factors such as changes in stomach contents and hydration status. Growth rate from hatching to sexual maturity in reptiles is typically initially linear, before beginning to plateau (Andrews, 1982). This was the case for our data, enabling us to use a simple measure of growth rate:

$\frac{SVL(24\, weeks) - SVL(hatching)}{elapsed\, weeks}$. Further, overall body condition (i.e. relative body mass) at hatching and 24 weeks of age was calculated by taking the residuals from a linear model of SVL and mass. We recorded deaths in the population for 24 weeks and subsequently quantified the proportion of each group surviving at the conclusion of each week to estimate survival curves.

For both sprint speed and bite force, each lizard was tested at 16 weeks post-hatching during two trials on separate days which consisted of at least two repeated measures per trial. Individuals were not tested for both bite force and sprint speed on the same day. Trials were conducted in the middle of the light cycle (i.e. afternoon) to maximise the likelihood that they had reached their optimal body temperature and reduce variance in temperature. Body temperature was recorded via a thermocouple in the cloaca and the small variation in body temperature did not predict maximum bite force or sprint speed, therefore it was subsequently dropped from analyses (sprint speed: $\chi^2 = 104.34$, *d.f.* = 136, $p = 0.98$; bite force: $\chi^2 = 23.87$, *d.f.* = 145, $p = 1$). To quantify morphometric variation relevant to performance, we measured the following morphological characters: head width at the widest point of the head, head length from the tip of the snout to the posterior of the jaw bone, head depth at the deepest point, jaw length from the tip of the snout to the last supralabial scale, hind limb length from the body wall to the edge of the foot pad, and SVL. All measurements were made using digital callipers to the nearest 0.01 mm. Head dimensions (width, length, depth, jaw) and hind limb length values were regressed against SVL and the residuals were retained for use in subsequent analyses. Principal components analysis (PCA) was performed on the residuals of head dimension measurements to obtain one dimension representing the greatest variance in head shape (principal component 1, PC1). PC1 explained 39.0% of variance and was driven primarily by head length and width (Table S1).

Sprint trials were conducted in a 115 cm × 10 cm × 20 cm (L × W × D) racetrack on a 30° incline with 80-grit sandpaper as substrate to provide traction and to resemble natural substrate (i.e. rock). A shelter, identical to that provided in their enclosure, was provided at the end of the racetrack. If reluctant to run, lizards were induced to run by gently tapping on the hindquarters using a paintbrush. Trials were filmed using a Canon EOS 600D camera (Canon U.S.A., Inc., Lake Success, NY) at 50 frames per second and subsequently analysed; all trials were conducted and analysed by one observer (C.M.D.). Interval speeds were calculated to 0.01 cm/s over each 10 cm section of the track from trials where the lizard ran continuously for ≥50 cm. Maximum interval speed from between four to six replicates per individual was retained for analysis.

In vivo bite forces were measured using an isometric Kistler Type 9203 force transducer mounted on a vertical holder and connected to a Kistler Type 5995A charge amplifier (Kistler Inc., Winterthur, Switzerland). Thin metal plates (i.e. bite plates) were attached to the force transducer and padded with medical tape on the outer surfaces to prevent damage to the teeth. The mouth of the lizard was opened by gently pulling on the gular region. The open jaws were placed onto the bite plates at the midway point of jaw length to standardize the point of force exertion; the position and angle of the head was kept as similar as possible across individuals (Lappin & Jones, 2014). This provoked voluntary forceful biting, otherwise the side of the mouth was tapped softly to induce biting. At least three recordings were taken per individual and the highest value was retained as the maximum bite force (Herrel et al., 1999).

Confirmation of paternity

Maternity was known for all offspring; however, paternity was not known due to multiple mates, and the potential for sperm storage and multiple paternity within clutches in the genus *Ctenophorus* (Hacking et al., 2017; Lebas, 2001; Mats Olsson et al., 2007, 2009; Uller et al., 2013). To confirm paternity, we genotyped adults and offspring at five microsatellite loci previously developed for *C. decresii sensu lato* (Ctde45, Ctde05, Ctde12; McLean et al. 2014) or *C. pictus* and *Amphibolurus muricatus* (CP10 and AM41, respectively; Schwartz et al. 2007). We collected blood for genetic samples by venipuncture from the sinus angularis in the corner of the mouth. Genomic DNA was extracted using an E.Z.N.A. Tissue DNA Kit (Omega Bio-tek, Norcross, GA, USA) and sent to the Australian Genome Research Facility (Melbourne, Victoria, AUS) for PCR amplification, fragment visualization and size calling. Paternity was assigned using CERVUS v 3.0.7 (Kalinowski et al., 2007; Marshall et al., 1998) which employs a maximum likelihood approach to assign the most likely candidate sire based on the genotypes of parents and offspring by estimating a likelihood-of-difference (LOD) score. First, we conducted a simulation of parentage analysis with the parameters of 50,000 offspring, 1% error rate, 5 candidate fathers, 95% of loci typed, and a minimum of 4 loci typed. Following this, we conducted a paternity analysis based on the trio (mother, father, and offspring) LOD score and a strict 95% confidence level (following Rankin et al. 2016). These were manually confirmed as likely fathers based on breeding pairings. To prevent researcher bias, paternity was confirmed following the conclusion of growth and performance data collection.

Statistical analyses

We conducted a linear discriminant analysis (LDA) to assess differentiation between the four classes of offspring (i.e. pure *C. decresii*, pure *C. modestus*, hybrids sired by *C. decresii* males, hybrids sired by *C. modestus* males). Offspring class was used as a dependent variable with fitness traits as independent variables (offspring class ~ bite force + sprint speed + growth rate + body condition at 24 weeks + body condition at hatching). Data were centred, scaled, and analysed using the R package *MASS* (v7.3.50; Ripley, 2002).

We used linear mixed models to examine the effects of parental species on parental reproductive traits (clutch size, embryonic mortality, seasonality of mating, egg mass at oviposition), offspring fitness traits (offspring mass at hatching, growth rate, bite force, sprint speed, body condition), and offspring morphology (SVL, hind limb length residuals, PC1 for head dimensions). Maternal species, paternal species, and their interaction were included as fixed terms and unique identifiers for the mother, father, and clutch were included as random-effect terms (response ~ maternal species + paternal species + maternal species*paternal species + (1|maternal_ID) + (1|paternal_ID) + (1|clutch_ID)). For body condition, growth rate, bite force, and sprint speed, offspring sex and its interactions with parental species were included as fixed terms (response ~ maternal species + paternal species + sex + maternal species*paternal species + maternal species*sex + paternal species*sex + maternal species*paternal species*sex + (1|maternal_ID) + (1|paternal_ID) + (1|clutch_ID)). For model simplification, we removed non-significant interactions with sex. We examined the residuals of each model for significant departures from normality and transformed the data if necessary. A Tukey-adjusted least-squares means for pairwise comparisons *post hoc* analysis was performed if an interaction term was statistically significant. One outlier was removed for clutch size and mass (8 eggs from a southern female which required medical intervention to remove them).

To investigate differences in sex ratios, we fitted a generalised linear mixed model with a binomial distribution and checked the data for overdisperson. Offspring sex was the response variable, parental species (maternal and paternal) and their interaction were fixed terms, and clutch ID was a random-effect term (sex ~ maternal species + paternal species + maternal species*paternal species + (1|clutch_ID)).

We examined the relationship between egg mass and hatchling mass based on maternal species using linear regression. To estimate total investment in egg production (i.e. fecundity) over the breeding season, we used the sum of egg masses produced by a female over the breeding season and fit a linear model with fecundity as the response variable and species as a fixed term. Desiccated clutches were included in this analysis only; to extrapolate, we assumed egg mass was the mean egg mass per clutch for each species because maternal SVL was not correlated with average egg mass in *C. modestus* ($F_{1, 15} = 0.01$, $p = 0.924$, $r^2 = 0.001$, slope ± SE = -0.001 ± 0.01) or *C. decresii* ($F_{0.3, 9} = 0.33$ $p = 0.582$, $r^2 = 0.035$, slope ± SE = 0.013 ± 0.02).

To examine offspring survival, we estimated survival curves using the Kaplan-Meier method and compared using a log-rank test (i.e. Mantel-Haenszel test) using the R packages *survival* (Therneau, 2015), and *survminer* (Kassambara & Kosinki, 2018).

Lastly, to investigate differences in adult male (sire) testes mass between species, we ran a linear model with testes mass as the response variable and species and SVL, and their interaction, as predictors (testes ~ species + SVL + species*SVL). The interaction was non-significant and was removed for model simplification.

All statistical analyses were conducted in R v. 3.5.1 (R Core Team 2018) using packages *factoMineR* (Lê et al., 2008), *MASS* (Venables & Ripley, 2002), *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), and *lsmeans* (Lenth, 2016) unless otherwise stated.

Results

Offspring fitness

Linear discriminant analyses (LDA) showed significant differentiation between the four offspring classes (pure *C. modestus*, pure *C. decresii*, *C. modestus* ♀ × *C. decresii* ♂, *C. decresii* ♀ × *C. modestus* ♂; Wilks' λ = 0.545, $F_{18,331} = 4.4$, $p < 0.0001$; Figure 2). LDA showed differentiation by paternal species along the first axis (LD1; variance explained = 53.5%; Figure 2), which was primarily driven by body condition at 24 weeks of age, bite force, and body condition at hatching (Table 1). The second axis (LD2) showed differentiation (variance explained = 43.9%) between maternal species driven primarily by growth rate, sprint speed, and body condition at hatching (Table 1; Figure 2). Correspondingly, univariate analyses revealed significant main effects of maternal species on growth rate and sprint speed, and effects of paternal species on bite force and body condition at 24 weeks of age in offspring (Table 2). Offspring produced by *C. modestus* females had a higher growth rate in the initial 24 weeks ($p < 0.001$; Table 2; Figure 3a; Figure S1) and had higher maximum sprint speeds ($p = 0.007$; Table 2; Figure 3b; Figure S1). Offspring sired by *C. decresii* males had higher maximum bite forces ($p = 0.025$; Table 2; Figure 3c; Figure S1) whereas those sired by *C. modestus* males had higher body condition at 24 weeks of age ($p = 0.004$; Table 2; Figure 3d; Figure S1).

There were no significant interactions between parental species for offspring fitness traits (growth rate, survival to 24 weeks, bite force, sprint speed, body condition) or morphological characters (SVL, hind limb length residuals, PC1 for head dimensions), indicating that these traits did not differ for pure and hybrid offspring. Additionally, there were no significant effects of parental species on body condition at hatching ($p > 0.05$; Table 2). There was a significant effect of sex on growth rate, bite force, body condition at hatching where measures for males were higher than for females (all $p < 0.05$; Table 2, Figure S2). Survivorship curves were not significantly different between offspring classes or by any combination of parental species ($p = 0.89$; Figure 3e; Table S2). Parental species did not influence any morphological traits ($p > 0.05$; Table S3).

Parental reproductive traits

All females were reproductively active: *C. modestus* females produced 32 clutches comprising 169 eggs and *C. decresii* females produced 21 clutches comprising 90 eggs. Of these, 5 clutches (29 eggs) and 7 clutches (27 eggs) produced by *C. modestus* and *C. decresii* females respectively were found desiccated outside of the nest box and excluded from all analyses except of fecundity. A higher proportion of *C. modestus* females multi-clutched with 66.7% and 11.1% laying second and third clutches respectively, whereas 23.5% of *C. decresii* females laid a second clutch and none laid a third clutch.

There were no significant interactions between parental species for reproductive fitness traits (fecundity, clutch size, embryonic mortality, egg mass at oviposition, and offspring mass at hatching), indicating that these traits did not differ for pure and hybrid pairings (Table 2; Figure S3). However, maternal species affected all of these traits (Table 2). Female *C. modestus* had overall higher fecundity over the breeding season ($p = 0.016$; Figure 4a). Female *C. modestus* also produced larger clutches ($p = 0.042$; Table 2; Figure 4b) with lower embryonic mortality ($p = 0.021$; Figure 4c). Female *C. decresii* produced heavier eggs ($p < 0.0001$; Figure 4d) and correspondingly heavier hatchlings ($p < 0.0001$; Figure 4e). Additionally, for the relationship between egg and hatchling mass, there was a steeper slope and stronger correlation for *C. decresii* females (slope ± SE = 1.12 ± 0.09, $r^2 = 0.84$) than for *C. modestus* females (slope ± SE = 0.60 ± 0.06, $r^2 = 0.72$, $p < 0.0001$; Figure 4f).

Overall, 76.2% and 52.4% of *C. modestus* and *C. decresii* males were reproductively successful, siring 26 and 27 clutches total, respectively. There was no significant difference in adult male testes mass between the species (Table 2; Figure 4g). We detected a 2.4% rate of multiple paternity, occurring in one out of the 41 clutches genotyped. Specifically, a clutch produced by a *C. modestus* female was sired by two *C. modestus* males which were paired with the female consecutively in one reproductive cycle and fathered 40% and 60% of the clutch respectively. This low rate of multiple paternity is comparable to the 4.3% rate of multiple paternity estimated from a wild population of *C. modestus* (one out of 23 clutches; Hacking et al. 2017). Additionally, there was a significant effect of paternal species on sex ratios of clutches ($p = 0.003$; Table 3; Figure 4h; Figure S3) where clutches sired by *C. modestus* males had a sex ratio skewed towards males (1:1.64 female:male) whereas clutches sired by *C. decresii* males had a sex ratio skewed towards females (1:0.69 female:male) at an incubation temperature of 28°C.

Discussion

Empirical assessments of reproductive incompatibility and hybrid fitness are essential to interpret genomic patterns observed across naturally occurring contact zones. Previous studies of the contact zone between *Ctenophorus decresii* and *C. modestus* revealed a hybrid swarm with predominantly *C. modestus* mtDNA haplotypes and genetic incompatibilities when backcrossing to *C. decresii* (Dong et al., 2019). In order to investigate intrinsic reproductive barriers, we conducted captive-breeding experiments between individuals from pure populations nearest to the contact zone and measured offspring fitness traits. We found that *C. modestus* and *C. decresii* females differed in maternal reproductive investment and strategy, irrespective of the species of their mate. *Ctenophorus modestus* females exhibited higher fecundity over the breeding season and produced larger clutches with lower individual egg masses and more clutches per season;

whereas *C. decresii* females produced fewer, smaller clutches with higher individual egg masses. Maternal and paternal species also influenced measures of offspring fitness; but hybrid offspring did not exhibit higher or lower fitness relative to pure offspring for individual fitness traits. However, the combination of traits inherited from maternal and paternal species could result in fitness differences among hybrid classes. Specifically, *C. modestus* ♀ × *C. decresii* ♂ hybrids may exhibit higher overall fitness due to the combination of higher growth rates, sprint speeds, and bite forces. The cumulative differences in maternal reproductive strategy and parental effects on fitness could contribute to genetic patterns observed across the contact zone between *C. modestus* and *C. decresii*.

Differences in maternal reproductive output may have broad ecological and evolutionary effects on populations by influencing offspring survival and fitness. Females of *C. modestus* produced a greater number of smaller offspring relative to *C. decresii* females, and this difference in maternal reproductive strategies reflects a fundamental reproductive trade-off between the number and size of eggs, with total clutch mass functionally constrained (Brockelman, 1975; Kaplan & Cooper, 1984; Smith & Fretwell, 1974). Egg and offspring size are intertwined with a range of factors such as survival and growth rate, and have fitness consequences due to the size-dependent nature of performance traits (Sinervo, 1990b, 1993). Additional differences in embryonic mortality, egg and hatching mass relationship, and sex ratio likely reflect differences in other unmeasured underpinning traits (e.g. yolk volume and content, gestation period, selection on incubation conditions). The differing reproductive strategies of the species could be the result of climate-driven selection. Climatic conditions of the higher latitudinal range of *C. decresii* (i.e. colder, temperate conditions) may place seasonal time constraints on their breeding season, restricting the time for embryo development and resulting in a higher investment in the first clutch. Comparatively, the range of *C. modestus* extends to a lower latitude (i.e. warmer, semi-arid conditions), which may allow for multi-clutching.

Maternal and paternal reproductive traits together may contribute to the prevalence of the *C. modestus* mtDNA haplotype within the contact zone. Based on our data, we estimate that the number of offspring produced by *C. modestus* females is at least 2–3 fold higher and with lower rates of embryonic mortality than *C. decresii* females. Additionally, in the context of hybrid crosses within the contact zone, *C. modestus* ♀ × *C. decresii* ♂ crosses will result in a higher proportion of female offspring that will pass on *C. modestus* mtDNA; however, this may vary with differing incubation conditions in the wild. A similar pattern was found following gene flow between fishes (*Gambusia affnis* and *G. holbrooki*) where differences in parental life-history traits confer a competitive advantage (i.e. body size, growth rates, age at sexual maturity) to progeny with *G. holbrooki* maternal parentage (pure and F1 offspring; Scribner 1993). This competitive advantage correlated to patterns in experimental and natural populations where *G. holbrooki* mtDNA predominated (Scribner, 1993; Scribner & Avise, 1994). Similarly, hybrids of mulberry species (*Morus rubra* and *M. alba*) with *M. alba* maternal genotypes have a strong fitness advantage, whereas paternal genotype has no effect on fitness (Burgess & Husband, 2004). Further exploration is needed, but these maternal effects are predicted to influence the genetic composition of the hybrid zone between *M. rubra* and *M. alba*.

Contrary to our predictions, hybrids did not differ from pure offspring in individual fitness traits. Nonetheless, there was some evidence of differentiation between reciprocal hybrid classes when considering the full complement of fitness traits. Hybrids sired by *C. decresii* males had higher growth rates and sprint speeds (*via* maternal influences) and higher bite forces (*via* paternal influence). Pure *C. modestus* offspring had higher growth rates and sprint speeds but lower bite forces; pure *C. decresii* offspring had lower growth rates and sprint speeds but higher bite forces; and hybrids sired by *C. modestus* males had lower growth rates, sprint speeds, and bite forces. Based on combined traits, pure *C. modestus* may have higher fitness than pure *C. decresii* (higher values of both axes in the multivariate analysis of fitness); however, the relative fitness of parental and hybrid classes ultimately depends on how the traits we measured during early ontogeny affect adult fitness in the wild. Exogenous factors (e.g. genotype-environment interactions) may significantly influence the survival of reciprocal F1 hybrids, even in the absence of genomic incompatibilities (Kimball et al., 2008).

The fitness traits we measured are ecologically relevant and indicative of survival and reproductive success. Higher growth rates are likely advantageous given the direct effects on factors such as body size and age at sexual maturity (Andrews, 1982; Ballinger, 1983). Differences in growth rates, exclusive of exogenous influences, are likely to reflect genetic differences in physiology and/or behaviour (Dawson, 1975; Hutchinson & Maness, 1979; Porter & Travy, 1983; Sinervo, 1990a; Sinervo & Adolph, 1989). Further, performance traits (i.e. bite force and sprint speed) are tightly linked with competitive ability in ecologically relevant tasks such as predator evasion (survivorship), foraging and prey capture, and the ability to acquire and defend territories (social dominance and reproductive success) in reptiles (locomotor performance: Garland, Jr. et al. 1990; Jayne and Bennett 1990; Robson and Miles 2000; Lailvaux et al. 2004; Perry et al. 2004; Husak 2006; Husak et al. 2006; Peterson and Husak 2006; reviewed in Husak and Fox 2008; bite force: Lailvaux et al. 2004; Huyghe et al. 2005; Lappin and Husak 2005; Anderson et al. 2008; Husak et al. 2009). These traits may be especially important determinants of male fitness in species with a polyandrous mating system where there is little evidence of female choice, such as *C. decresii and C. modestus*.

Ctenophorus modestus ♀ × *C. decresii* ♂ F1 hybrids exhibited higher trait values for more fitness measures than remaining offspring including the reciprocal hybrid cross, *C. decresii* ♀ × *C. modestus* ♂. Given these patterns, the composition of the F2 generation may be dominated by *C. modestus* mtDNA (progeny of hybrids sired by *C. decresii* males and/or pure *C. modestus* offspring). This is consistent with the observed prevalence of hybrids with *C. modestus* mtDNA in the contact zone; however, this is speculative because our study was limited to F1 hybrids due to the generation time of the species (≥ 2 years until sexual maturity). However, F2 hybrids often suffer strong negative fitness effects (hybrid breakdown) when recessive DMIs are more likely to manifest and/or cytonuclear interactions are further disrupted (Burton et al., 2006; Edmands, 1999; Ellison et al., 2008; Stelkens et al., 2015; Xue et al., 2019). Fitness can be rescued by backcrossing to the maternal species to restore parental nuclear and mitochondrial combinations, whereas backcrossing to the paternal species perpetuates the mismatch (Ellison & Burton, 2008). This is a conceivable explanation for the observed extensive backcrossing to *C. modestus* by post-F1 hybrids which virtually all have *C. modestus* mtDNA (Dong et al., 2019). We cannot exclude the possibility of sterility or reduced fertility of F1 hybrids with *C. decresii* mtDNA and/or the contribution of exogenous selection. Another contributor could be the mate preference of F1 hybrid males for females with *C. modestus* mtDNA (pure or hybrid) and/or preference of *C. modestus* females for hybrid males; however, F1 hybrid mate preferences in this system are unknown. It is difficult to draw inferences about mating behaviours based on cytonuclear patterns in hybrids because a variety of factors may produce these patterns. In other systems, cytonuclear patterns in hybrids have been attributed to differences in the abundance of each sex (Malmos et al., 2001; Wirtz, 1999) or species (Burgess et al., 2005) in the hybrid zone, marked differences in body size which only allow certain combinations (Grant & Grant, 1997;

Karl et al., 1995), and postmating prezygotic barriers such as conspecific sperm precedence (Monsen et al., 2007).

In summary, our data indicate that differences in maternal reproductive investment and strategy, together with parental effects on offspring fitness and sex ratio differences, may contribute to patterns of genetic variation across the contact zone between *C. decresii and C. modestus*, particularly the prevalence of *C. modestus* mtDNA. Stronger intrinsic genetic incompatibilities between the two species may manifest primarily in the F2 generation. Nevertheless, our results highlight how divergence between parental species in reproductive traits, as well as effects on offspring fitness, can combine to shape contact zone dynamics.

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Data Accessibility

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.p5hqbzkp1

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Tables

Table 1. Standardised linear discriminant coefficients for the first two canonical variables showing discrimination between offspring classes. Characters strongly correlated with canonical variables (large absolute values) are bolded and italicised.

	LD1	LD2
Bite Force	***-0.531***	-0.107
Sprint Speed	0.385	***0.609***
Growth Rate	0.013	***0.620***
Body Condition at 24 Weeks	***0.831***	0.111
Body Condition at Hatching	***0.550***	***-0.577***
Proportion of variance	0.533	0.439

Table 2. Results of a linear model of female fecundity and species, and linear mixed-effects models investigating the effects of parental species on reproductive traits (embryonic mortality, egg mass at oviposition, offspring mass at hatching) and on offspring fitness traits (growth rate, maximum sprint speed, maximum bite force, body condition at hatching and 24 weeks of age). Statistically significant values are indicated with asterisks (* = *p* < 0.05, ** = *p* < 0.01, *** = *p* < 0.001).

Response	Fixed Term	Sum Sq	Mean Sq	*d.f.*	DenDF	*F*	*p*
Growth Rate	Maternal	0.13	0.13	1	36.37	5.14	0.029*
	Paternal	0.00	0.00	1	26.77	0.03	0.854
	M × P	0.01	0.01	1	39.16	0.41	0.527
	Sex	0.12	0.12	1	125.19	4.59	0.034*
Sprint Speed	Maternal	8370.10	8370.10	1	30.27	9.45	0.004**
	Paternal	2402.10	2402.10	1	25.08	2.71	0.112
	M × P	408.10	408.10	1	32.62	0.46	0.502
	Sex	1.30	1.30	1	114.35	0.00	0.970
Bite Force	Maternal	0.47	0.47	1	35.89	1.01	0.323
	Paternal	2.43	2.43	1	34.08	5.24	0.028*

	M × P	0.24	0.24	1	38.72	0.51	0.478
	Sex	2.70	2.70	1	128.55	5.82	0.017*
Body Condition at Hatching	Maternal	0.02	0.02	1	16.12	1.96	0.180
	Paternal	0.01	0.01	1	25.74	1.09	0.305
	M × P	0.00	0.00	1	24.94	0.37	0.547
	Sex	0.06	0.06	1	124.30	6.88	0.010**
Body Condition at 24 Weeks	Maternal	0.02	0.02	1	19.49	0.12	0.737
	Paternal	1.30	1.30	1	22.40	9.91	0.005**
	M × P	0.06	0.06	1	57.72	0.46	0.501
	Sex	0.06	0.06	1	125.24	0.43	0.511
Fecundity	Species	99.71	99.713	1	-	6.46	0.016*
Clutch Size	Maternal	4.01	4.01	1	16.62	4.83	0.042*
	Paternal	0.50	0.50	1	19.95	0.60	0.448
	M × P	0.71	0.71	1	33.29	0.85	0.363
Embryonic	Maternal	0.32	0.32	1	22.81	6.11	0.021*
	Paternal	0.06	0.06	1	31.37	1.14	0.295
	M × P	0.03	0.03	1	31.37	0.50	0.486
Egg Mass	Maternal	0.11	0.11	1	28.37	21.72	< 0.0001***
	Paternal	0.00	0.00	1	40.69	0.88	0.355
	M × P	0.00	0.00	1	40.69	0.22	0.642
Hatchling Mass	Maternal	0.06	0.06	1	26.53	21.11	< 0.0001***
	Paternal	0.00	0.00	1	40.44	0.49	0.489
	M × P	0.00	0.00	1	40.44	0.06	0.808
Testes Mass	SVL	0.03	0.03	1	-	7.15	0.012*
	Species	0.0003	0.0003	1	-	0.06	0.812

†M x P = Maternal x Paternal

Table 3. Results of a generalised linear model investigating the effects of parental species on offspring sex ratio. Statistically significant values are indicated with asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Response	Fixed Term	*d.f.*	χ^2	*p*
Sex	Maternal	1	0.424	0.515
	Paternal	1	8.637	0.003**
	Maternal x Paternal	1	2.362	0.124

Figure legends

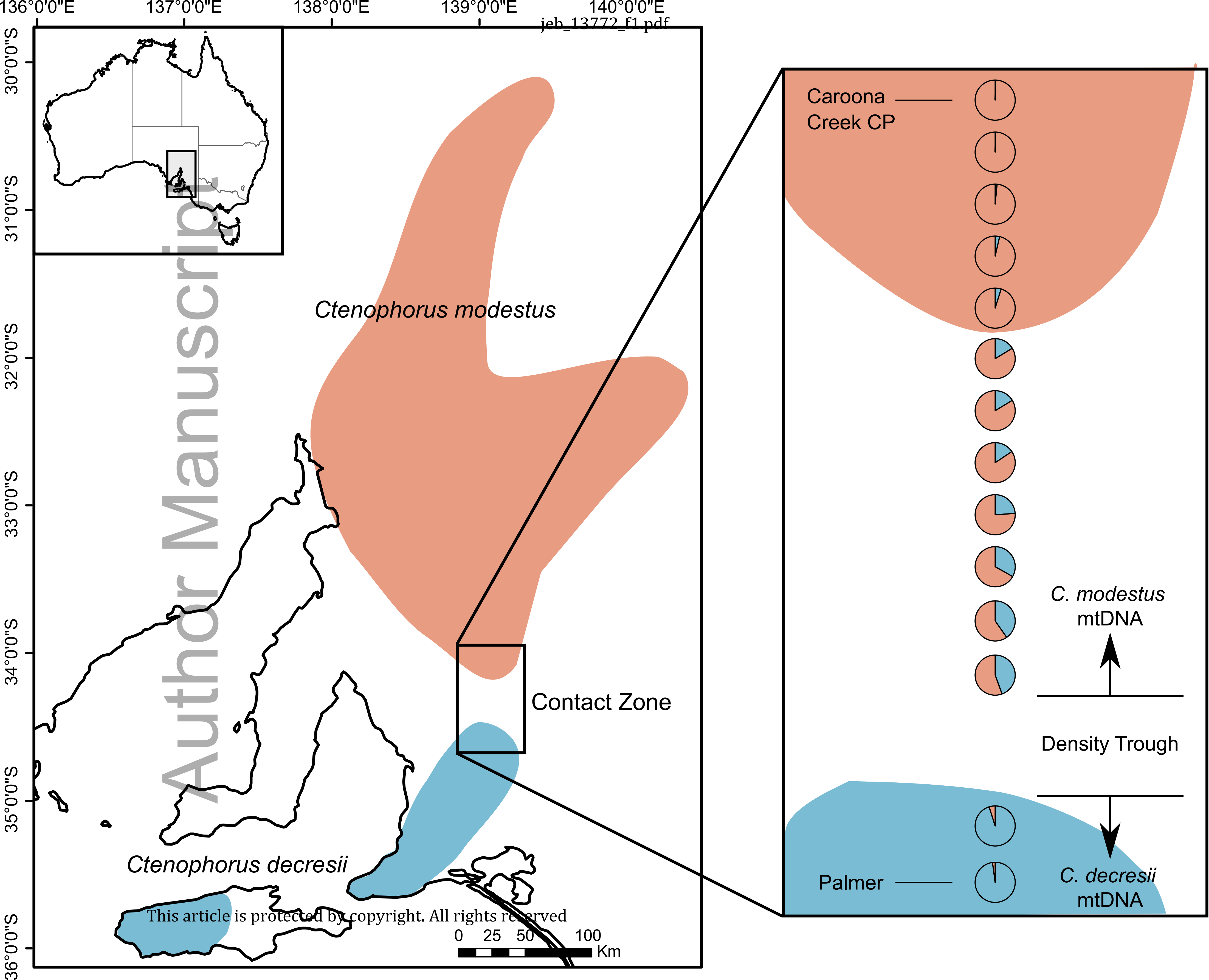
Figure 1. The distributions of *Ctenophorus modestus* (shaded orange; previously northern lineage *C. decresii sensu lato*) and *C. decresii* (shaded blue; previously southern lineage *C.*

decresii sensu lato) and an enlarged map section of the contact zone. Pie charts show mean proportion of genome inherited from each parental species (i.e. hybrid index) for 14 sites along a linear transect through the contact zone. An approximately 12-km density trough where multi-year surveys recovered no individuals, and whether sites contain *C. modestus* or *C. decresii* mitochondrial (mtDNA) haplotypes, is indicated. Genetically pure sites from which individuals were sourced for captive breeding anchor each end of the contact zone transect: Caroona Creek Conservation Park (CP; *C. modestus*) and Palmer (*C. decresii*).

Figure 2. Linear discriminant analyses of offspring classes based on five fitness variables: sprint speed, bite force, growth rate, body condition at 24 weeks, body condition at hatching. Linear discriminant 1 (LD1) is positively associated with body condition (at hatching and 24 weeks of age) and negatively associated with bite force; linear discriminant 2 (LD2) is positively associated with growth rate and sprint speed, and negatively associated with body condition at hatching (Table 1). 95% confidence ellipses are shown.

Figure 3. Species differences in measures of F1 hybrid offspring fitness. (a) Growth rate over the initial 24 weeks and (b) maximum sprint speed by maternal species; (c) maximum bite force and (d) body condition at 24 weeks of age by paternal species; (e) survival curves over the initial 24 weeks estimated using the Kaplan-Meier method by offspring class [H (m-d) = *C. modestus* ♀ × *C. decresii* ♂ hybrids, H (d-m) = *C. decresii* ♀ × *C. modestus* ♂ hybrids]. Statistically significant values are indicated with asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Figure 4. Species differences in parental reproductive traits: (a) fecundity (i.e. total reproductive output during the breeding season), (b) clutch size, (c) embryonic mortality, (d) egg mass, (e) hatchling mass, and (f) relationship between egg and hatchling masses by maternal species with regression line, (g) testes mass adjusted for SVL by male species, and (h) sex ratio by paternal species. Statistically significant values are indicated with asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).


136°0'0"E
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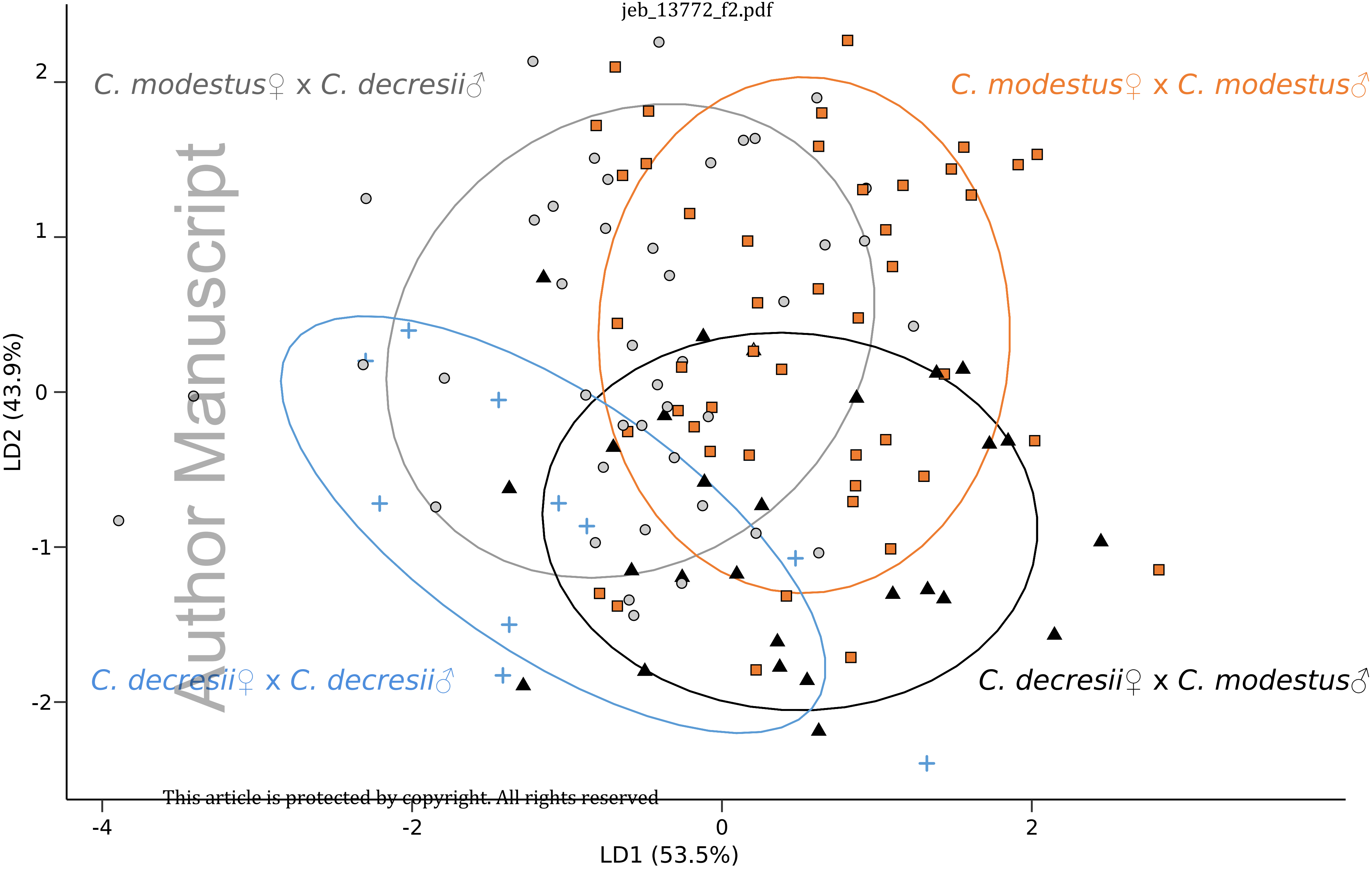
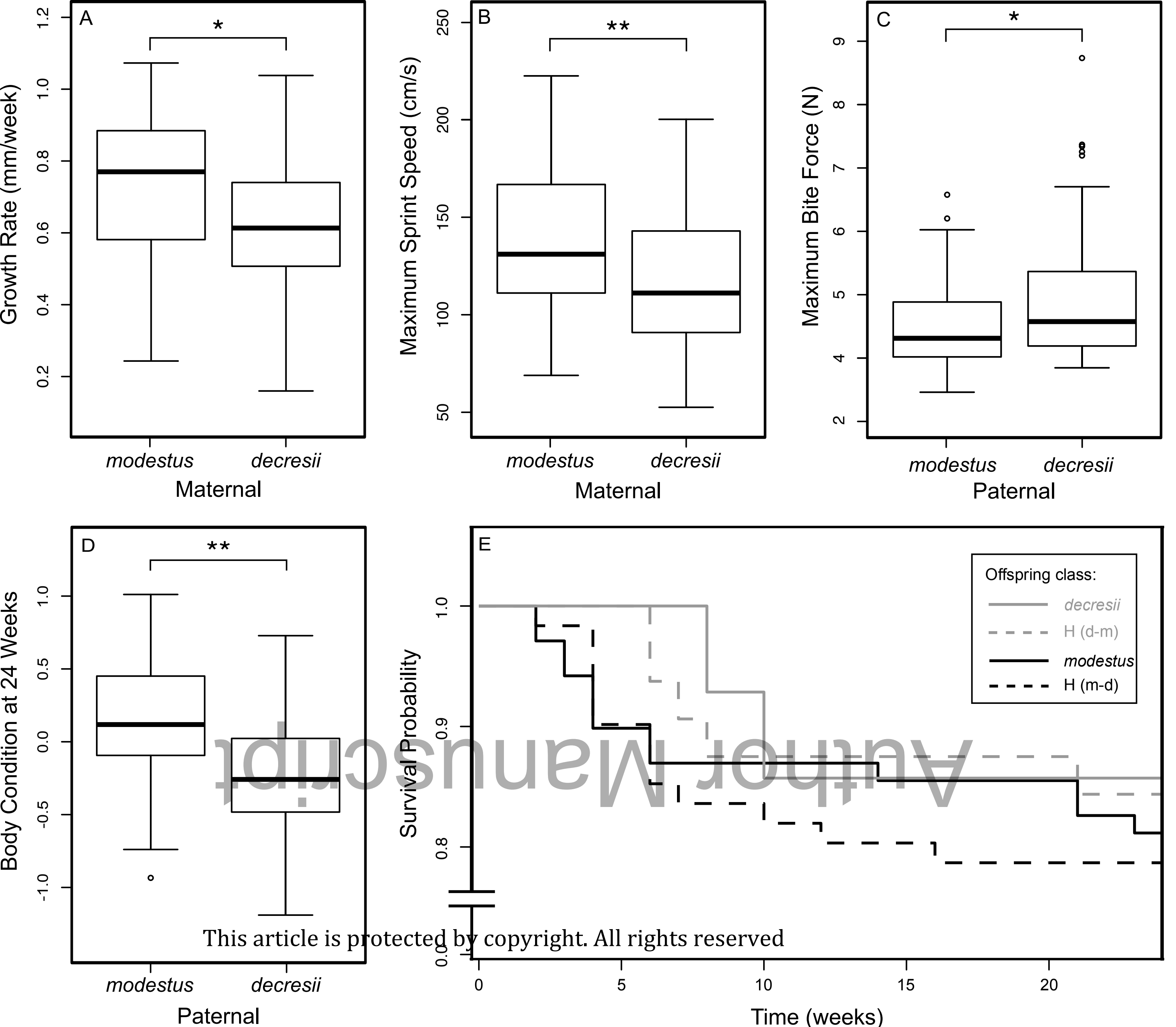
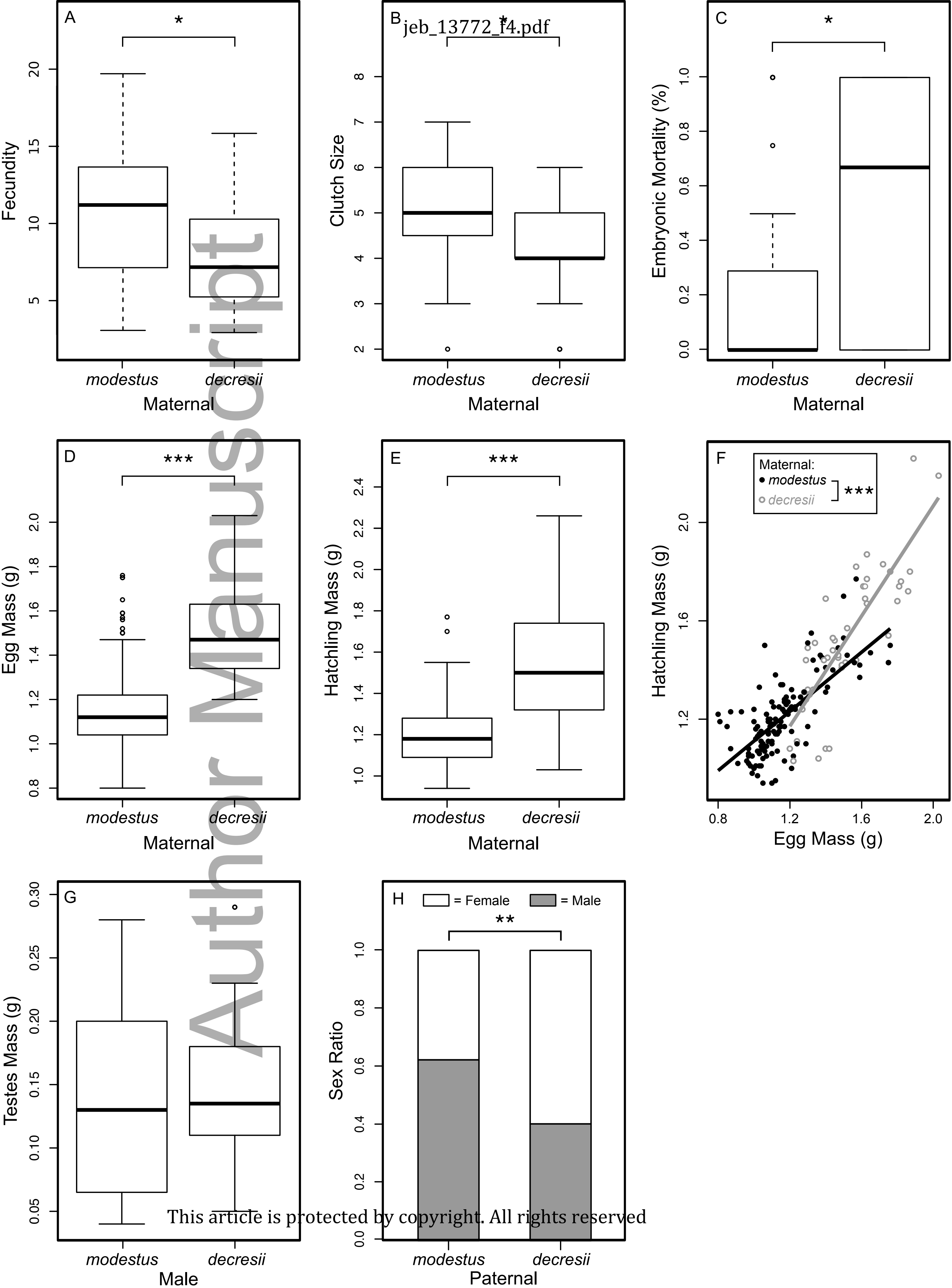
Ctenophorus modestus
Contact Zone
Ctenophorus decresii
0 25 50 100
Km
Caroona
Creek CP
C. modestus
mtDNA
Density Trough
Palmer
C. decresii
mtDNA


C. modestus♀ x C. decresii♂
C. modestus♀ x C. modestus♂
C. decresii♀ x C. decresii♂
C. decresii♀ x C. modestus♂
LD2 (43.9%)
2
1
0
-1
-2
LD1 (53.5%)
-4
-2
0
2


A
*
Growth Rate (mm/week)
0.2
0.4
0.6
0.8
1.0
1.2
modestus
decresii
Maternal
B
**
Maximum Sprint Speed (cm/s)
50
100
150
200
250
modestus
decresii
Maternal
C
*
Maximum Bite Force (N)
2
4
5
6
7
8
9
modestus
decresii
Paternal
D
**
Body Condition at 24 Weeks
-1.0
-0.5
0.0
0.5
1.0
modestus
decresii
Paternal
E
Offspring class:
decresii
H (d-m)
modestus
H (m-d)
Survival Probability
0.0
0.8
0.9
1.0
Time (weeks)
0
5
10
15
20


A
*
Fecundity
5
10
15
20
modestus
decresii
Maternal
B
*
Clutch Size
2
3
4
5
6
7
8
modestus
decresii
Maternal
C
*
Embryonic Mortality (%)
0.0
0.2
0.4
0.6
0.8
1.0
modestus
decresii
Maternal
D
***
Egg Mass (g)
0.8
1.0
1.2
1.4
1.6
1.8
2.0
modestus
decresii
Maternal
E
***
Hatchling Mass (g)
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
modestus
decresii
Maternal
F
Maternal:
● modestus
○ decresii
***
Hatchling Mass (g)
1.2
1.6
2.0
0.8
1.2
1.6
2.0
Egg Mass (g)
G
Testes Mass (g)
0.05
0.10
0.15
0.20
0.25
0.30
modestus
decresii
Male
H
□ = Female
▨ = Male
**
Sex Ratio
0.0
0.2
0.4
0.6
0.8
1.0
modestus
decresii
Paternal