

**Online Supplement**

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**Eavesdropping micropredators as dynamic limiters of sexual signal elaboration and intrasexual competition**

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**Supplementary Videos.** Recordings from 2010 and 2012 of calling male túngara frogs (*Engystomops pustulosus*). Most movies feature males being attacked by frog-biting midges (Diptera: Corethrellidae) and their anti-midge defensive swats. The size of the inflated vocal sac relative to the length of the frog's arm prevents the male from swatting while calling.

**Table S1.** Local model structures for the global piecewise structural equation model.

Model formula	Error structure	Link
swats ~ midges + (1   date) + (1   ID)	Poisson	sqrt
midges ~ chucks + rival males + (1   date) + (1   ID)	Poisson	sqrt
call rate ~ rival males + swats + midges + (1   date)	Gaussian	identity
chucks ~ rival males + (1   date)	Gaussian	identity

**Table S2.** Local model structures for the piecewise structural equation model (SEM) in which the directionality between chucks and midges was reversed from the global piecewise SEM.

Model formula	Error structure	Link
swats ~ midges + (1   date) + (1   ID)	Poisson	sqrt
midges ~ rival males + (1   date) + (1   ID)	Poisson	sqrt
call rate ~ rival males + swats + midges + (1   date)	Gaussian	identity
chucks ~ rival males + midges + (1   date)	Gaussian	identity

**Table S3.** Local model structures for the piecewise structural equation model in which the effects of rival males were removed.

Model formula	Error structure	Link
swats ~ midges + (1   date) + (1   ID)	Poisson	sqrt
midges ~ chucks + (1   date) + (1   ID)	Poisson	sqrt
call rate ~ swats + midges + (1   date)	Gaussian	identity
rival males ~ 1	NA	NA

**Table S4.** All direct, indirect and total effects from the global piecewise structural equation model (SEM) without rival males.

Direct, indirect and total effects of structural equation model paths		
Effect	Path	Std. Estimate
Direct	Chucks → Midges	-0.129
	Midges → Call rate	-0.090
	<b>Midges → Swats</b>	<b>0.756</b>
	<b>Swats → Call rate</b>	<b>-0.306</b>
Indirect	Midges → Call rate (via Swats) (Midges → Swats) * (Swats → Call rate)	-0.231
Total	Midges → Call rate (Midges → Swats) * (Swats → Call rate) + (Midges → Call rate)	-0.321

Note. – The standardized estimates were derived using the relevant range approach. Rows in bold indicate significant direct effects. The piecewise SEM analysis did not test the statistical significance of indirect nor total effects.

**Table S5.** Local model structures for the piecewise structural equation model in which the effects of midges and anti-midge swatting were removed.

Model formula	Error structure	Link
swats ~ 1	NA	NA
midges ~ 1	NA	NA
call rate ~ rival males + (1   date)	Gaussian	identity
chucks ~ rival males + (1   date)	Gaussian	identity

**Table S6.** Results of Shipley's test of directed separation for each piecewise structural equation model (SEM).

piecewise SEM	Fisher's <i>C</i>	df	<i>P</i> -value	AICc	$\Delta$ AICc
Global w/o rival males	3.252	6	0.777	35.020	0.000
Global	0.524	2	0.769	50.378	15.358
Global w/ chucks $\leftarrow$ midges	0.524	2	0.769	50.378	15.358
Global w/ chucks $\leftarrow$ midges; chucks $\leftarrow$ swats	0.524	2	0.769	53.821	18.801
Global w/o midges & swats	25.342	6	0	–	–
Initial	11.041	4	0.026	–	–

Note. – *P*-values that are greater than the significance level of  $\alpha = 0.05$  indicate that the hypothesized relationships stipulated in the model are consistent with the observed data. Piecewise SEMs that exceed the significance threshold are compared using AICc values.

**Table S7.** All direct, indirect and total effects from the global piecewise structural equation model (SEM).

Direct, indirect and total effects of structural equation model paths		
Effect	Path	Std. Estimate
Direct	Rival males → Call rate	0.078
	<b>Rival males → Chucks</b>	<b>0.221</b>
	Rival males → Midges	0.026
	Chucks → Midges	-0.144
	Midges → Call rate	-0.089
	<b>Midges → Swats</b>	<b>0.756</b>
	<b>Swats → Call rate</b>	<b>-0.300</b>
Indirect	Rival males → Midges (via Chucks) (Rival males → Chucks) * (Chucks → Midges)	-0.032
	Rival males → Call rate (via Midges) (Rival males → Midges) * (Midges → Call rate)	-0.002
	Rival males → Call rate (via Midges & Swats) (Rival males → Midges) * (Midges → Swats) * (Swats → Call rate)	-0.006
	Rival males → Call rate (via Chucks & Midges) (Rival males → Chucks) * (Chucks → Midges) * (Midges → Call rate)	0.003
	Rival males → Call rate (via Chucks & Midges & Swats) (Rival males → Chucks) * (Chucks → Midges) * (Midges → Swats) * (Swats → Call rate)	0.007
	Midges → Call rate (via Swats) (Midges → Swats) * (Swats → Call rate)	-0.227
Total	Rival males → Midges (Rival males → Chucks) * (Chucks → Midges) + (Rival males → Midges)	-0.006
	Rival males → Call rate [(Total Effect: Rival males → Midges) * (Midges → Swats) * (Swats → Call rate)] + [(Total Effect: Rival males → Midges) * (Midges → Call rate)] + (Rival males → Call rate)	0.080
	Midges → Call rate (Midges → Swats) * (Swats → Call rate) + (Midges → Call rate)	-0.316

Note. – The standardized estimates were derived using the relevant range approach. Rows in bold indicate significant direct effects. The piecewise SEM analysis did not test the statistical significance of indirect nor total effects.

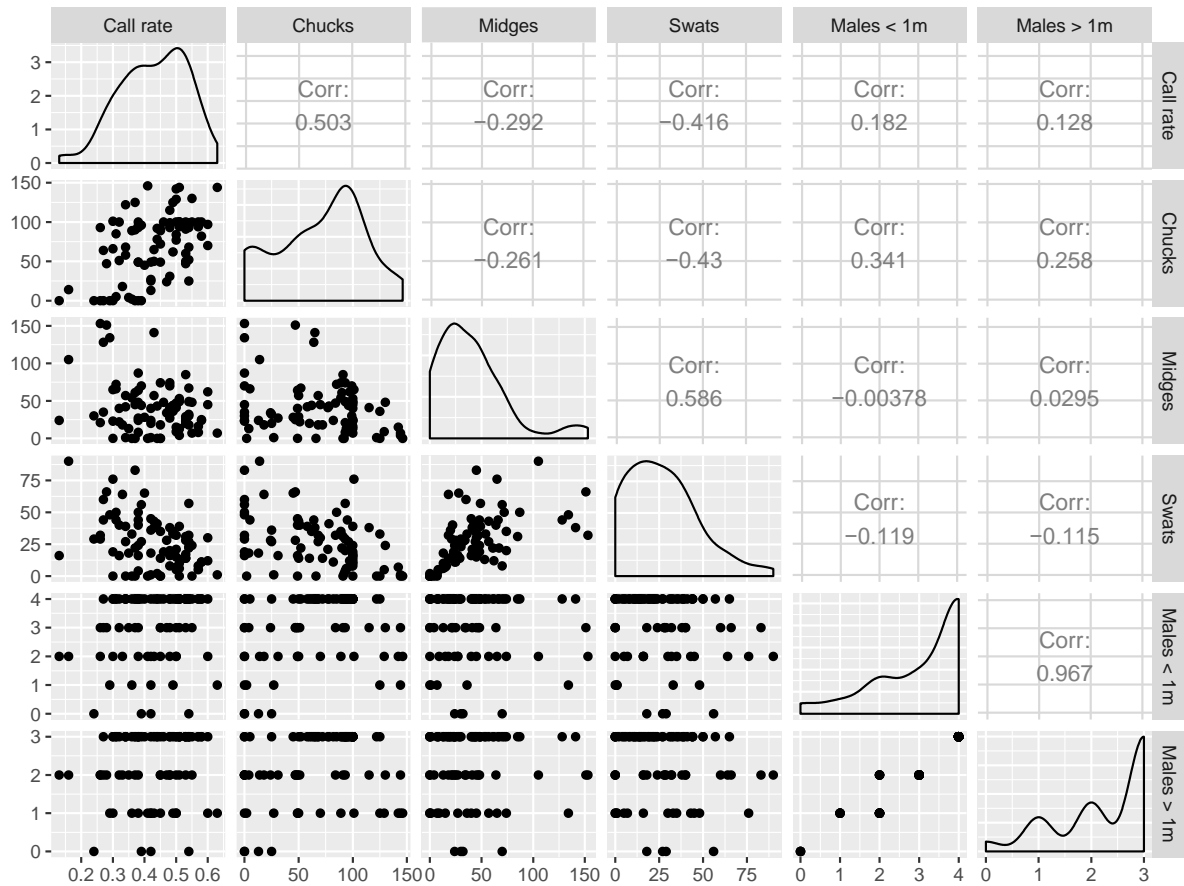
**Table S8.** Local model structures for the piecewise structural equation model (SEM) in which, compared to the global piecewise SEM, 1) the directionality between chucks and midges was reversed, and 2) the correlated error relationship between swats and chucks was replaced with a direct effect of swats on chucks.

Model formula	Error structure	Link
swats ~ midges + (1   date) + (1   ID)	Poisson	sqrt
midges ~ rival males + (1   date) + (1   ID)	Poisson	sqrt
call rate ~ rival males + midges + swats + (1   date)	Gaussian	identity
chucks ~ rival males + midges + swats + (1   date)	Gaussian	identity

**Table S9.** Comparison of unstandardized effects between global structural equation model (SEM) and SEM that incorporates a direct, causal effect of a male's swatting on his propensity to append chucks to his calls.

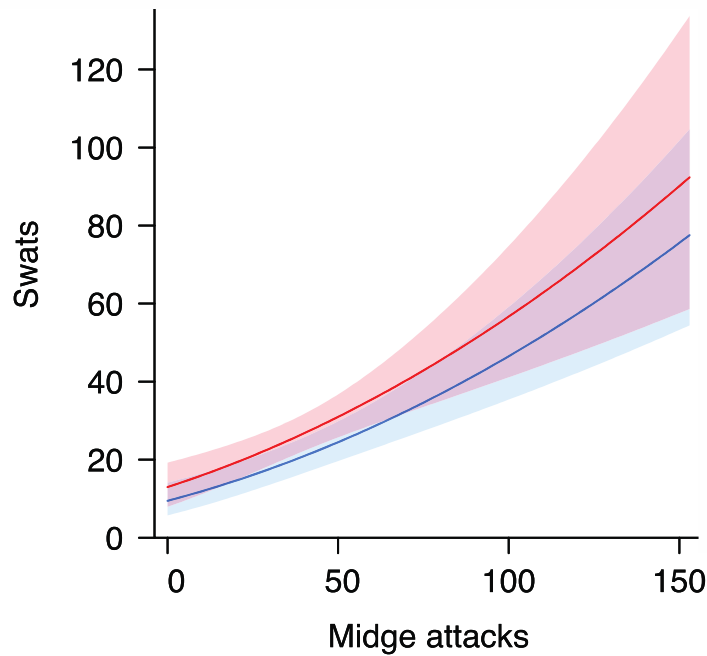
Path	Unstandardized path estimate	
	SEM w/ midges → chucks	SEM w/ midges → chucks; swats → chucks
Rival males → Call rate	0.010 ± 0.010	0.010 ± 0.010
Rival males → Chucks	<b>8.056 ± 3.741</b>	<b>8.273 ± 3.617</b>
Rival males → Midges	-0.121 ± 0.295	-0.121 ± 0.295
Midges → Chucks	-0.104 ± 0.113	0.022 ± 0.132
Midges → Call rate	0.000 ± 4e-04	0.000 ± 4e-04
Midges → Swats	<b>0.037 ± 0.006</b>	<b>0.037 ± 0.006</b>
Swats → Call rate	<b>-0.002 ± 6e-04</b>	<b>-0.002 ± 6e-04</b>
Swats → Chucks	NA	<b>-0.516 ± 0.235</b>
Call rate ~~ Chucks	<b>0.336</b>	<b>0.359</b>
Swat count ~~ Chucks	-0.175	NA

Note. – Values are the unstandardized path estimates ± standard error. Significant effects are shown in bold. For paths, arrows denote direct effects while double tildes denote correlated errors.



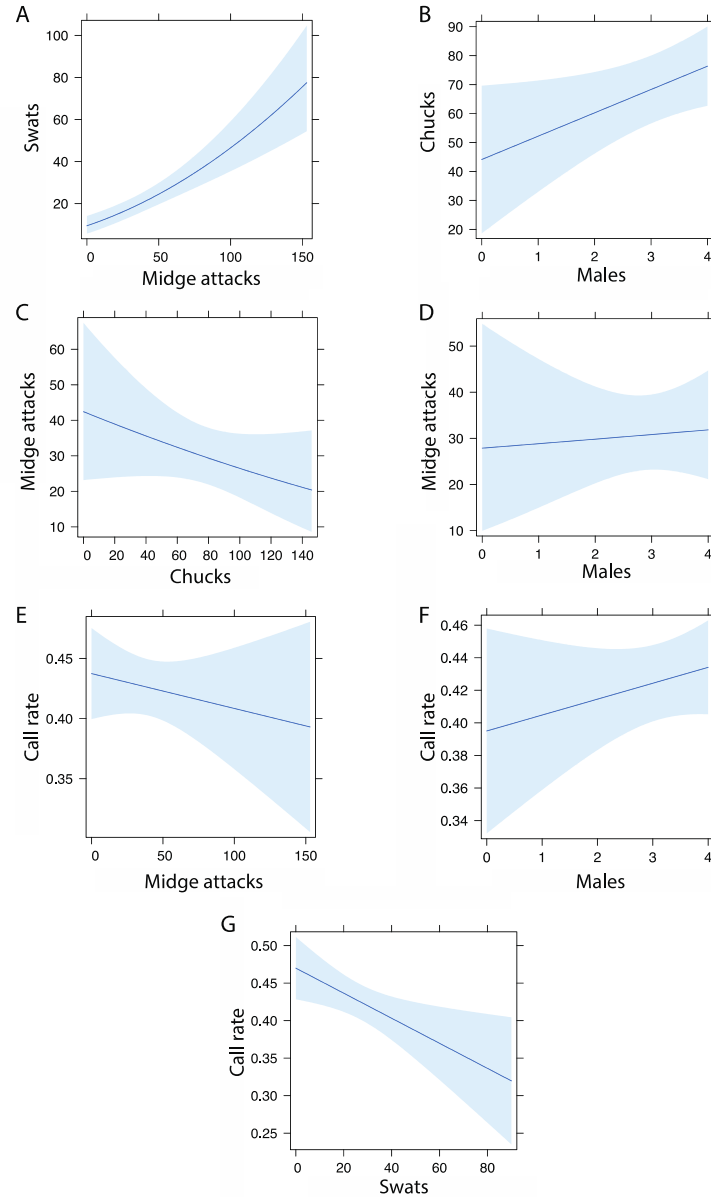
**Figure S1.** Matrix plot of behavioral data from 85 focal male túngara frogs. Scatterplots are shown in the lower left section, Pearson correlation coefficients are shown in upper right section and distributions of each variable are shown along the diagonal. Variables: “Call rate” is the total number of calls, minus one, divided by the time from the beginning of the first call to the beginning of the last; “Chucks” is the total number of chucks over the 50 sequential calls; “Midges” is the total number of frog-biting midges observed landing on the focal frog over 50 sequential calls; “Swats” is the total number of swats observed over the 50 sequential call duration; “Males < 1m” is the number of neighbor male competitors present within 1 meter of focal frog; “Males > 1m” is the level of observer’s perceived abundance of calling conspecifics beyond 1 meter of focal frog (0 = only focal frog heard calling, 1 = individual calling frogs could be counted, 2 = calls of frogs overlapping but individuals distinguishable, 3 = full chorus, cannot distinguish individuals). See

R code for matrix plot that also includes date and total duration of call sequence (Leavell et al. 2021).

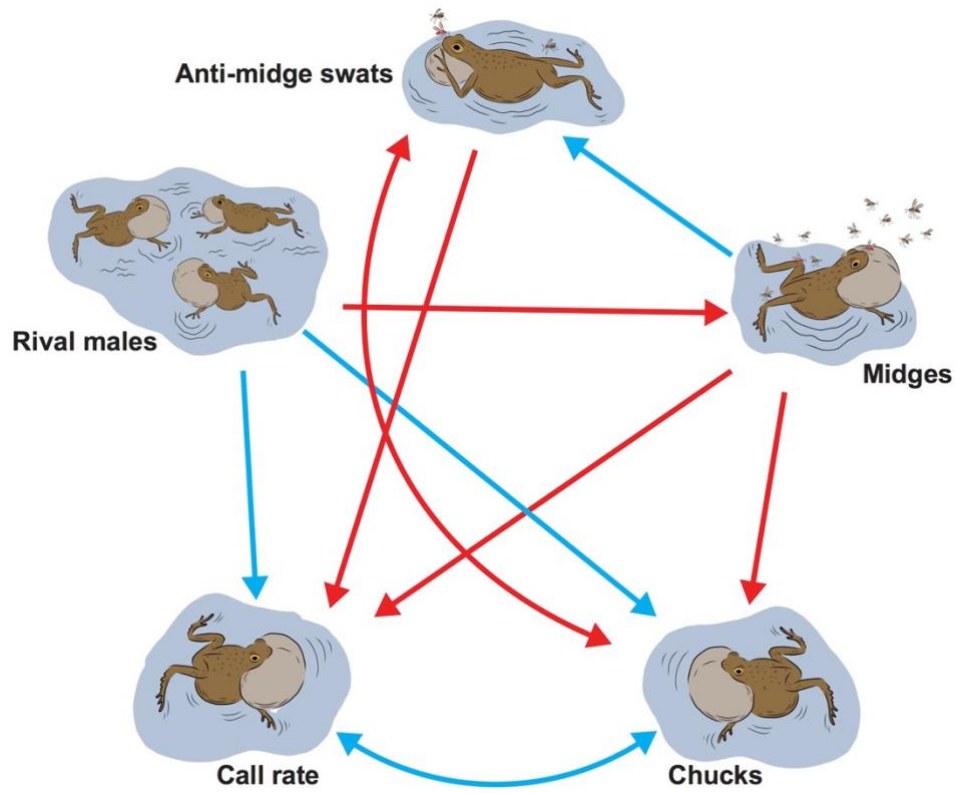


**Figure S2.** Comparison of effect plots between local-level swat model used in piecewise structural equation models (SEM) and hurdle model. Fitted regressions (solid lines) of the effect of midge attacks on a focal male's total number of anti-midge swats, with 95% confidence intervals (shaded areas). The output from the local-level swat model used in the piecewise SEMs is in blue. Red indicates the output from the hurdle model. The  $x$ -axis is restricted to the range of observed values.

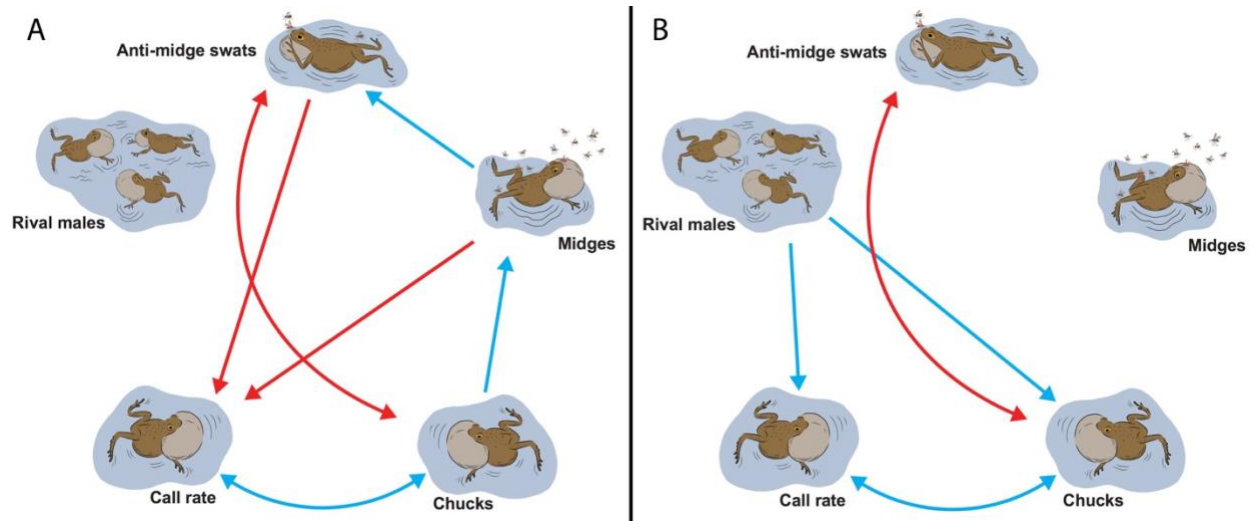




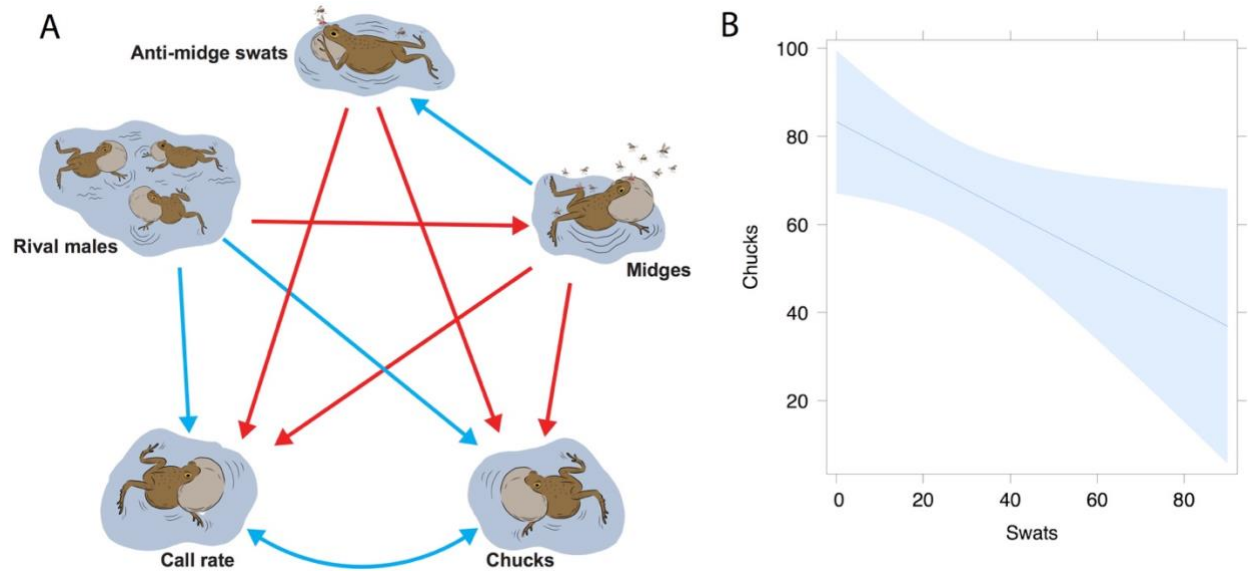
**Figure S3.** Local-level effect plots from global piecewise structural equation model (SEM). Panels display fitted partial regression functions (solid lines), with all other parameters in the local-level model fixed at mean values, and 95% confidence intervals (shaded areas). The  $x$ -axes are restricted to the ranges of observed values. The four local models here show the effects on a focal male's total number of anti-midge swats (A), total number of complex 'chucks' appended to calls (B), the total number of attacks by frog-biting midges (C-D) and call rate (E-G).



**Figure S4.** Network of hypothesized causal processes with midges as a predictor of the focal male's number of chucks. Blue and red paths indicate positive and negative effects, respectively. Single-headed arrows represent direct effects, while double-headed arrows represent partial correlations. All paths match those specified in the global model, with the exception of the path between midges and chucks, which is reversed. Illustrations by Razi Hedström.



**Figure S5.** The hypothesized causal pathways of two alternative piecewise structural equation models (piecewise SEM). A) Hypothesizes that only the intensity of attacks by frog-biting midges, and their influence on anti-midge swats, affects male call elaboration. B) Hypothesizes that only intrasexual competition affects male call elaboration. Direct effects and partial correlations are illustrated by single- and double-headed arrows, respectively. Red paths indicate negative relationships; blue paths indicate positive relationships. Partial correlations between call rate and chucks, and anti-midge swats and chucks, are included in both models to match the global SEM. All variables shown in these networks are included in the SEMs to account for potential significant missing pathways in tests of directed separation. Illustrations by Razi Hedström.



**Figure S6.** A) The hypothesized causal paths for the piecewise structural equation model (SEM) that incorporates a direct effect of swats on chucks. B) A local-level effect plot from the same piecewise structural equation model (SEM) with all other parameters in the local-level model fixed at mean values. Note the fitted partial regression function (solid line) and 95% confidence intervals (shaded areas). The  $x$ -axis is restricted to the range of observed values. Illustrations by Razi Hedström.

### **Justifications for initial hypothesized causal paths**

#### ***Rival males → Call rate***

Male túngara frogs increase their call rate in response to increased numbers of calling males (Green 1990; Bernal et al. 2009a,b).

#### ***Rival males → Chucks***

Male túngara frogs dynamically modify the number of chucks they add per call in response to the calls of other male, typically by adding or removing a single chuck at a time (Bernal et al. 2009a; Goutte et al. 2010). Males that call alone typically produce calls without chucks, but add chucks to their calls when next to other calling males (Ryan 1985). Additionally, males call with more chucks per call as the number of males within 1m increase (Bernal et al. 2007).

#### ***Rival males → Midges***

Increases in the number of aggregated prey reduces an individual's predation risk via the dilution effect (Foster and Treherne 1981; Alem et al. 2011). Here, we predict that more neighbors will result in less midge attacks per frog. An assumption for this prediction is that each male attracts a similar number of midges. Differential attraction of midges within a group of up to three neighboring, calling túngara frogs has been shown to vary based on intermale differences in call elaboration (Aihara et al. 2016). The midges in the study that showed this effect, however, were collected prior to landing on their frog victims, making it unclear how anti-midge swatting might influence male calling behavior and subsequent midge foraging decisions among the competitors.

#### ***Chucks → Midges***

Midges prefer calls with chucks to calls without chucks (Bernal et al. 2006). Also, males that produce more chucks attract more midges (Aihara et al. 2016).

***Midges → Call rate***

Similar to how the threat sensitivity hypothesis (Sih 1986; Helfman 1989) predicts that defensive behaviors scale in intensity with risk, if males scale their calling behaviors in response to predation risk, then males should reduce calling rates, independent of swatting frequency, in response to greater numbers of midges. While call rate is also a predictor of midge attraction (Aihara et al. 2016), we did not include this relationship to meet the assumption of acyclic paths required for piecewise SEMs (Shipley 2009; Lefcheck 2016).

***Midges → Swats***

Following the threat sensitivity hypothesis (Sih 1986; Helfman 1989), males will swat more frequently in response to greater numbers of midge attacks.

***Swats → Call rate***

There is likely a temporal trade-off between swatting and calling, as males do not appear to be capable of performing both tasks simultaneously (Bernal and Leavell, pers. obs.; see Supplementary Videos). Thus, swatting should reduce an individual's call rate.

***Call rate partially correlated with Chucks***

Males often change their call rate and the number of chucks concomitantly (Green 1990; Bernal et al. 2009a). A previous study that also observed naturally calling male túngara frogs and attacking frog-biting midges found a negative interaction between call rate and number of chucks (Aihara et al. 2016). That is, when call rates were low, midges were more attracted to frogs that produced more chucks. Whereas, when males produced few chucks, midges were more attracted to males that called more frequently. As stated above, the midges that showed this effect, however, were collected prior to landing on their frog victims, making it unclear how midge-frog contact

and anti-midge swatting might influence male calling behavior and subsequent midge foraging decisions among the competitors.

### **Confirming the effect of midges on anti-midge swatting with hurdle model**

The local-level generalized linear mixed-effects model (GLMM) that modeled the effect of the number of midge attacks on a focal male's swat rate was zero-inflated, yet piecewiseSEM currently does not support zero-inflated nor zero-altered models. We instead validated the fit of the swat GLMM by comparing it with a separate model that accounted for zero-inflation. Because the zeros in the swat data were true zeros (i.e., were not the result of design, survey nor observer errors), we chose a two-part 'hurdle' model (Martin et al. 2005). This approach allowed us to account for true zeros by modeling the probability that a male does not swat, then separately modeling the effect of midge attacks on swatting males. The fixed effect (number of midge attacks) and random effect (date) matched the swat GLMM, but the hurdle model did not include frog identity as an observation-level random effect. We compared hurdle models with varying truncated error structures for the non-zero data and included either midge attacks or both midge attacks and the random effect of date in the zero-inflation formulas. All hurdle models were developed with *glmmTMB* (Brooks et al. 2017) and the top hurdle model was selected based on sample-size corrected Akaike information criterion (AICc) values using *bbmle* (Bolker and R Development Core Team 2020).



### **Investigating the potential direct effect of a male's swatting behavior on call complexity**

In natural settings, male túngara frogs in a chorus call in bouts that are temporally separated by sustained silence. The “ramping up” of call elaboration is generally seen at the onset of calling bouts, in which one or two males begin calling and then are joined gradually by other males in the chorus. This gradual escalation in the social environment is thought to drive the initial increase in call complexity (Bernal et al. 2009a).

It is possible that a male's own swat might cause a temporary reduction in the male's call complexity before he once again ramps up the number of chucks he adds to his calls. Such an effect and its underlying mechanism have not been empirically shown and thus require speculation, which is why the causal relationship between swats and chucks was not included in the global SEM. There is no reason, however, to dismiss this potential direct path in the analysis. In following our exploratory use of structural equation models and our aim to uncover potential alternative explanations of our observations which might guide future studies, we therefore examined how including a direct swat-chuck link might impact the conclusions of this study.

To examine this potential direct effect, we compared our existing SEMs with a new SEM in which we replaced the correlated error relationship between swats and chucks with a direct effect of swats on chucks (Figure S6A; Table S8). We could not modify the global SEM to include this effect because doing so violates the assumption of acyclic paths (Shipley 2009; Lefcheck 2016). We instead modified the SEM in which midges had a direct effect on chucks (Figure S4). As noted in the main text and in Table S6, the latter model's paths were otherwise identical to the global SEM and of equal fit as the global SEM ( $\Delta\text{AICc} = 0$ ;  $C_2 = 0.524$ ,  $P = 0.769$ ).

Shipley's test of directed separation for the new SEM that incorporated a causal swat-chuck link reveals an acceptable model-data fit ( $C_2 = 0.524$ ,  $P = 0.769$ ) and does not reveal a change in the significance nor magnitude of effects for other paths (Table S9). As expected, based on the analysis of our initial hypothesized SEM, swats had a significant, direct negative effect on the number of chucks a male adds to his calls (Figure S6B). Adding the direct effect of swats on chucks, however, penalizes the overall AICc score, such that the SEM had  $> 2 \Delta\text{AICc}$  compared to the global SEM, global SEM with the direct effect of midges on chucks, and global SEM without rival males (Table S6). These results indicate that adding a direct swat-chuck path does not better explain the observed data and does not have cascading effects on other paths in the network, thus reinforcing the initial conclusions of the study.

### Investigating a potential case of “Simpson’s paradox”

In the local-level linear mixed model (LMM) in which call rate was the dependent variable, the number of midge attacks paradoxically had an indirect negative effect on call rate (via swatting) while having no direct effect. As reversal of effects are known to occur when comparing different scales of analysis (Bickel et al. 1975), a phenomenon often referred to as “Simpson’s paradox” (McElreath 2020), we further investigated the relationship between midges, swats and call rate.

To evaluate the extent to which variance in call rate was originally explained by swats, we built a LMM with swats removed (i.e., only rival males and midge attacks are independent variables; see R code for details (Leavell et al. 2021)). In this second model, midges could only directly affect call rate. We developed this model strictly for statistical inference as such direct effect of midges on call rate is not in line with our causal hypotheses. The model shows that midges are now significant with a negative effect on call rate ( $P = 0.012$ ;  $\beta = -0.001$ ). The contrasts between the original and second call rate LMMs revealed that swats best explained the variance in call rate within our original LMM and incorporating midge attack as a variable added little extra explanation. This explains how an indirect, but not direct, effect of midge attacks on call rate resulted from the original SEM. We wondered if this result might be due to collinearity between swats and midge attacks. Yet, when assessing multicollinearity among variables in our original analysis, neither midge attacks nor male swat responses revealed evidence of high collinearity (i.e., GVIF < 3, per (Zuur et al. 2009); Lines 206-212), indicating that males vary in how they respond with swats to midge attack. Altogether, this result led us to pursue what might be driving variance in anti-midge responses by analyzing two potentially ecologically-relevant subgroups that might account for unexplained heterogeneity.

We first posited that Simpson's paradox might appear due to variation in a continuum between risk-prone and risk-averse behavior. When confronted with the same amount of midges, some males swat less or not at all (risk-prone) while others swat more frequently (risk-averse). We therefore assigned each frog to one of these categories based on the residuals from our generalized linear mixed model in which swats was the response variable and midge attacks was the only independent variable (date was, again, a random intercept). Frogs with data points that were negative residuals (i.e., swatting less than predicted based on the number of midge attacks) were assigned to "risk-prone" and positive residuals (i.e., swatting more than predicted based on number of midge attacks) were assigned to "risk-averse". Second, we evaluated whether frogs have different strategies based on the intensity of the attack. Specifically, we assessed if low vs. high-intensity midge attacks might affect a frog's call rate. Based on the scatter plot of swats as a function of midge attacks in Figure S1, it appears that a behavioral shift might occur at a threshold of 25 midges, as it is approximately at this intensity where among-individual variation in swat responses appears. We therefore decided to perform two separate analyses to evaluate the presence of subgroups with different behavioral responses. In the first analysis we used a threshold of 25 midges and for the second we chose the median value of 34 midge attacks to evenly separate "low" and "high" midge attack intensities.

For the analyses, we used LMMs with *i*) call rate as the dependent variable, *ii*) risk response (with levels "risk-prone" and "risk-averse"), midge attack intensity (with levels 0-25 and 25+, or 0-34 and 34+) and their interaction as independent variables, and *iii*) date as a random intercept. Using the "anova" function in the R package "lmerTest" (Type III ANOVA F-test with Satterthwaite's method) we found no significant effects for either variable nor their interactions:

ANOVA table (midge attack intensity threshold = 25 attacks)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
risk_response	0.0017336	0.0017336	1	74.52502	0.1926132	0.6620203
midge_attack_intensity	0.0047991	0.0047991	1	79.18215	0.5331949	0.4674217
risk_response:midge_attack_intensity	0.0001518	0.0001518	1	75.69964	0.0168695	0.8970036

ANOVA table (midge attack intensity threshold = 34 attacks)

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
risk_response	0.0015954	0.0015954	1	75.04445	0.1798087	0.6727508
midge_attack_intensity	0.0114309	0.0114309	1	74.79929	1.2883455	0.2599772
risk_response:midge_attack_intensity	0.0000317	0.0000317	1	80.28937	0.0035748	0.9524717

The original analysis considers *a priori* sources of heterogeneity (e.g., date), and we followed up by further exploring additional factors that could generate heterogeneity, thoroughly examining the data for factors that could result in different patterns at different scales and thus may be driving the paradox. These findings, however, do not show evidence supporting the phenomenon of Simpson's paradox. Despite the high variation, heterogeneity (composition from different components) is not at play as there do not seem to be subgroups that could generate different patterns at different scales.

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