

Coordinated singing in a pair-living primate: resource or mate defense?



Sofya Dolotovskaya

German Primate Center, Göttingen

Behavioral Ecology & Sociobiology Unit

Duetting

songs of two individuals alternate or overlap

most widespread in birds



in mammals, mainly found in primates



pair-living species with long-term pair bonds and year-round territoriality

usually male-female pairs



Chiroxiphia

sometimes joined by offspring



Why coordinate singing?

most bird studies: cooperative displays, benefits for both individuals

joint resource defense

advertise ownership of
territory/resources

mate defense

advertise own or partner's
mated status

pair-bond reinforcement

- paternity guarding
- female mate guarding
- defending own position from intruders

Titi monkeys

- Neotropics, ca. 30 species
- small groups: mated pair + offspring
- long-term pair bonds & territoriality
- biparental care, male carry infants
- male-female duets
- partially overlapping songs
- sometimes joined by offspring





Coppery titi monkeys, *Plecturocebus cupreus*

Estación Biológica Quebrada Blanco, Peruvian Amazon



Predictions

joint resource defense

songs more frequent / longer when:

- more fruits available
- more resources needed, e.g. pregnancy / lactation / bigger groups

songs concentrated around dawn

songs longer during inter-group encounters

mate defense (paternity guarding)

songs more frequent / longer when:

- females are receptive

pair-bond reinforcement

songs produced all day

songs not longer during inter-group encounters

Methods

8 habituated groups

June 2017 - September 2021, 490 obs. days

group scans every 10 min, incl. diet & GPS

all instances of coordinated singing

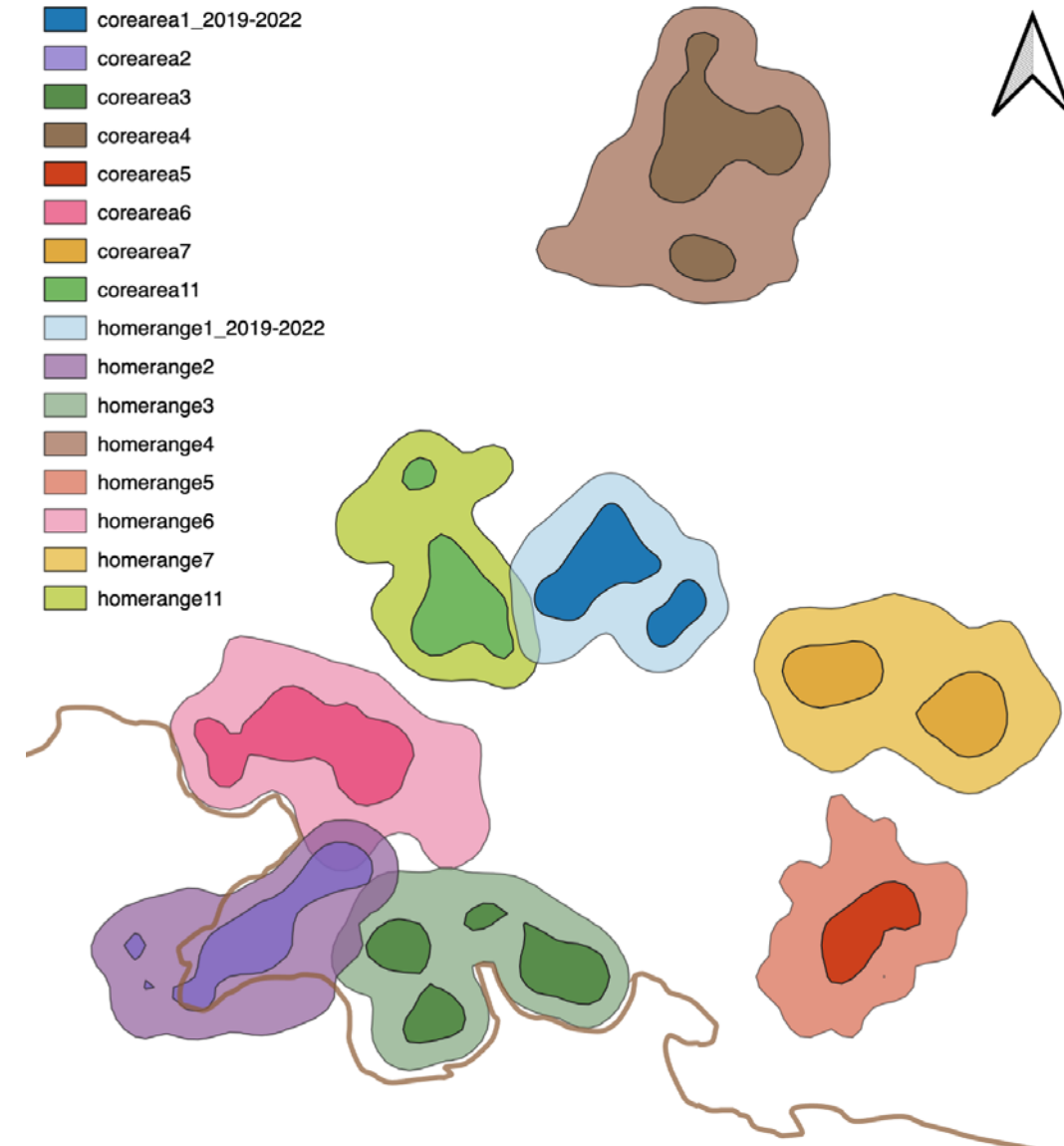
time, duration, context, GPS

female reproductive state:

data on infant births + copulations

fruit availability: mean monthly % feeding time

allocated to fruits as a proxy



Methods

Dataset 1: song presence/absence on observation days

227 days, 8 groups

are songs more frequent on days when:

- fruits consumed more intensively
- females receptive
- groups bigger ?

GLMM: song yes/no ~ female repr. state + fruit consumption + group size + rainfall + (1 | group ID)

Methods

Dataset 2: characteristics of songs

159 singings bouts, 8 groups

[singing bout: interrupted by pauses < 5min]

- are songs longer when:
 - fruits consumed more intensively
 - females receptive
 - produced during intergroup encounters ?

GLMM: song duration ~ female repr. state + fruit consumption + context + (1 | group ID)

- are songs distributed throughout home range?
- are songs concentrated around dawn?

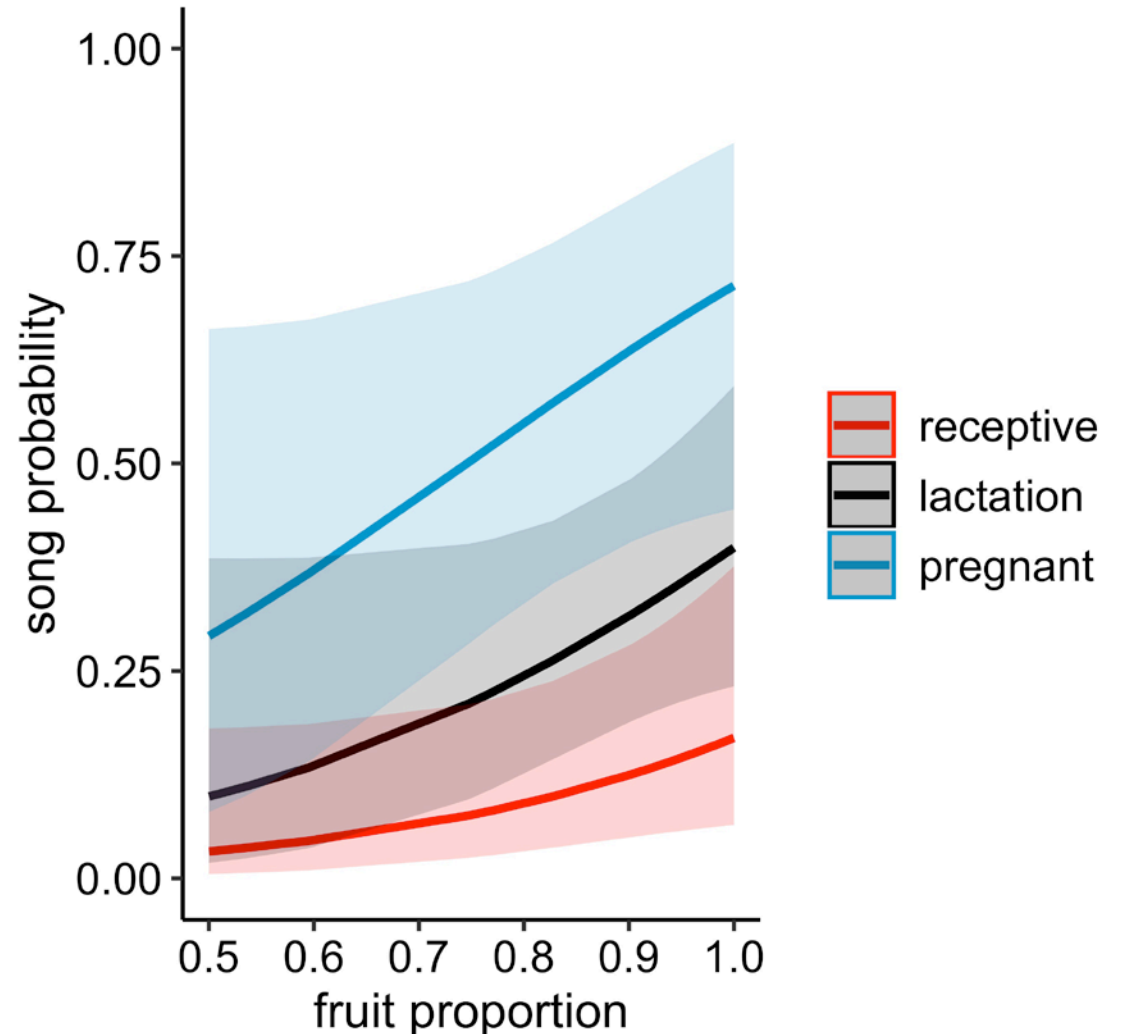
Results: What affected probability of singing?

✓ female reproductive state
full-reduced models: $\chi^2=15.697$, $df=2$, $P=0.0004$

± fruit consumption
full-reduced models: $\chi^2=3.442$, $df=1$, $P=0.064$

group size
full-reduced models: $\chi^2=1.471$, $df=1$, $P=0.225$

rainfall
full-reduced models: $\chi^2=0.189$, $df=1$, $P=0.664$



Results: What affected duration of singing?

✓ context

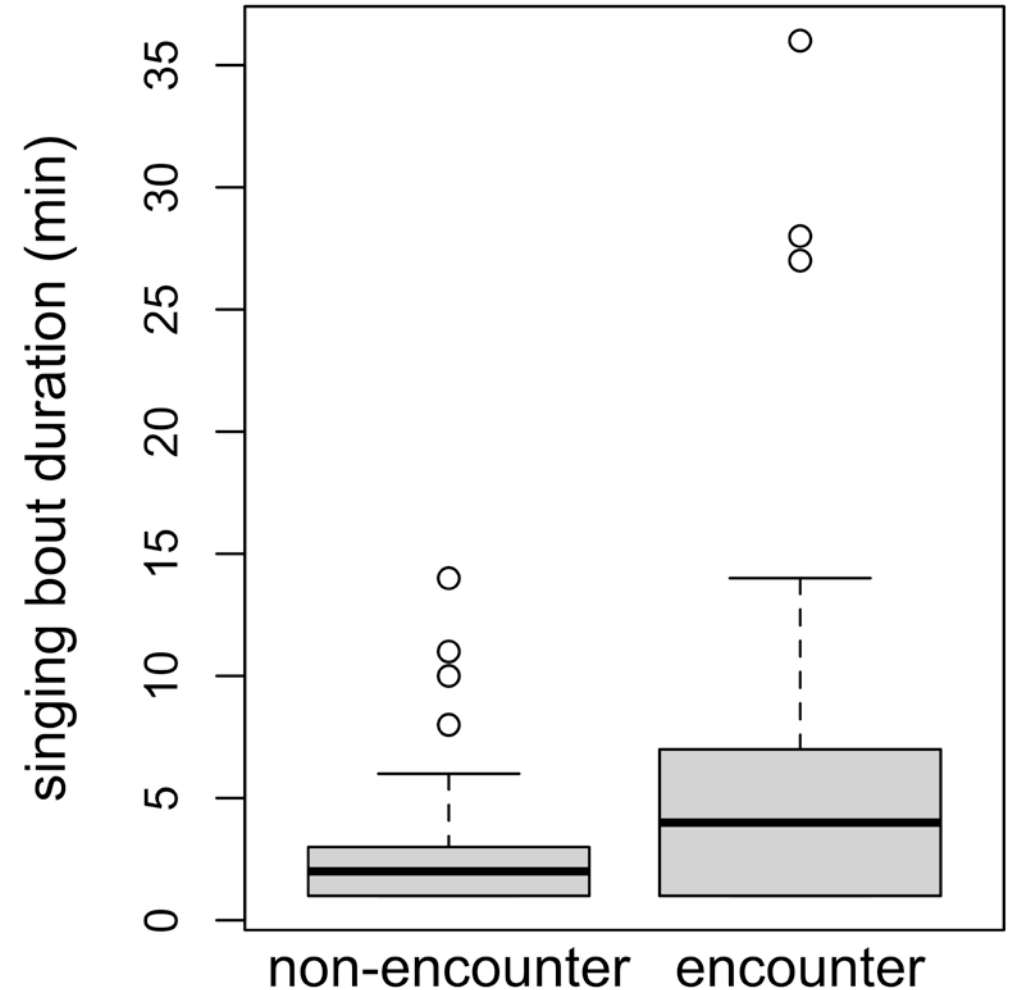
full-reduced models: $\chi^2=14.555$, $df=1$, **$P=0.0001$**

female reproductive state

full-reduced models: $\chi^2=1.024$, $df=2$, **$P=0.599$**

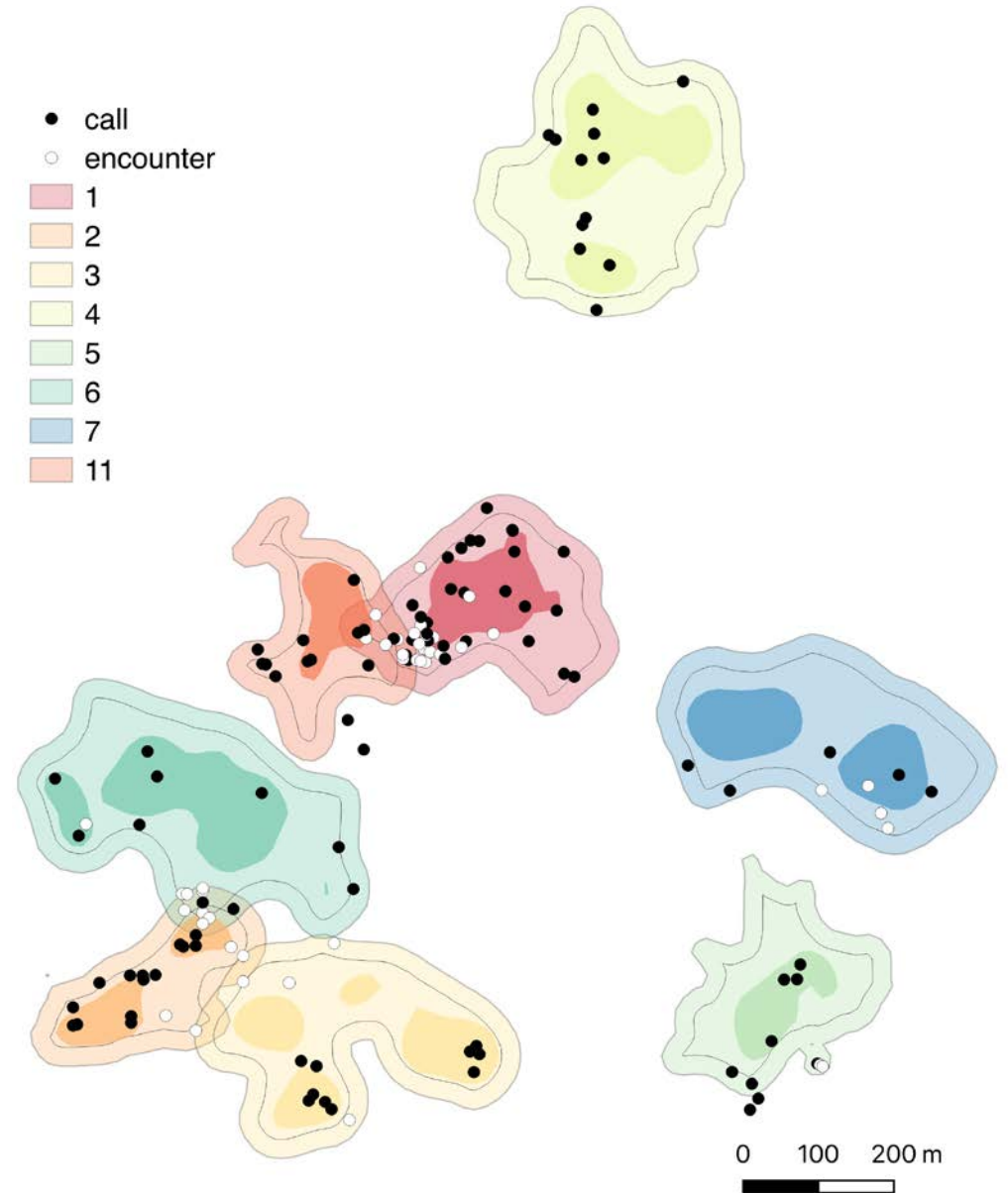
fruit consumption

full-reduced models: $\chi^2=0.948$, $df=1$, **$P=0.330$**



Results: Spatial distribution of songs

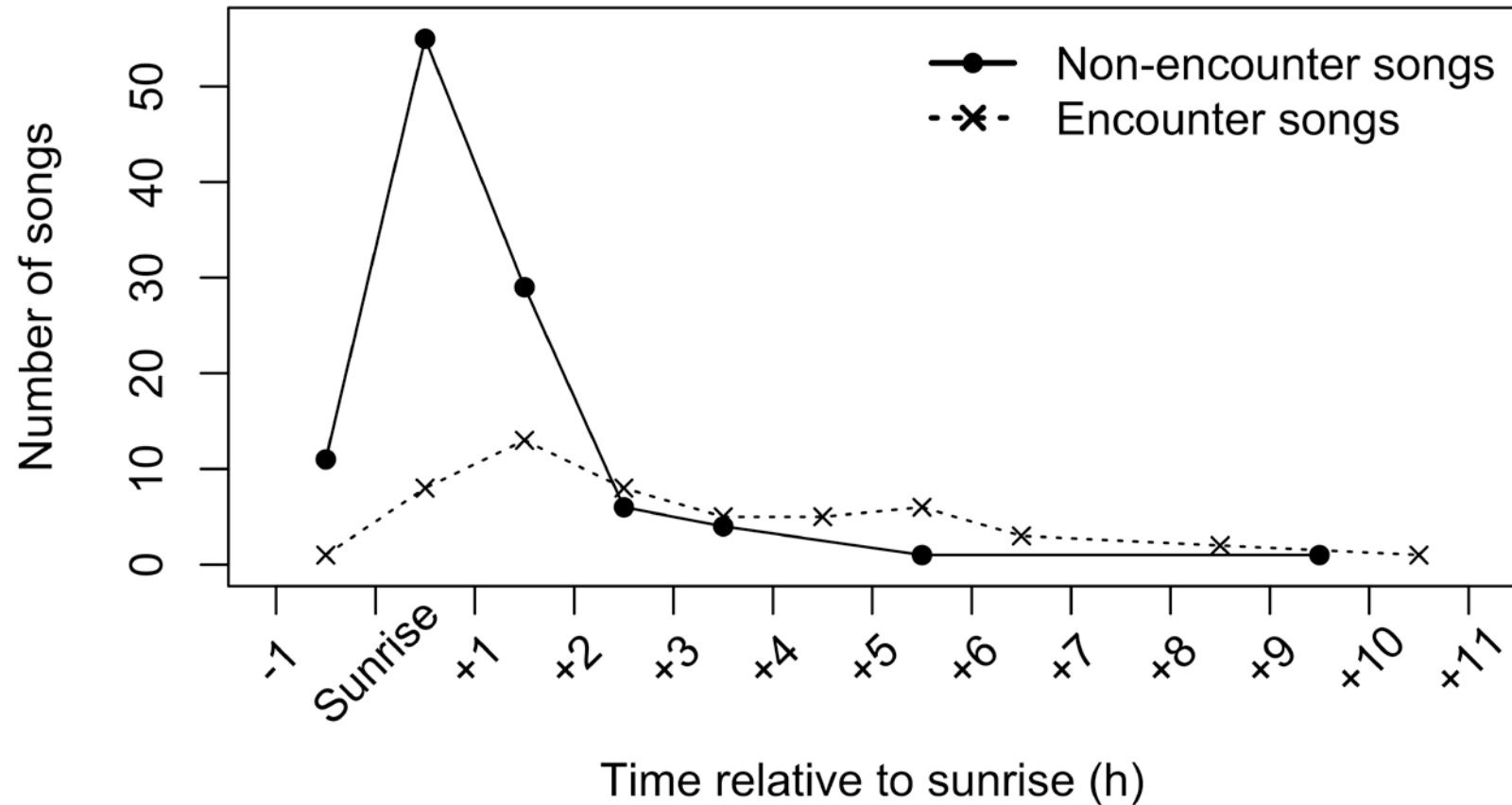
Songs distributed throughout home ranges
in concordance with its use



Observed vs. expected freq. of songs in core areas vs. rest of home range:
Fisher's tests: gr1 $P=0.094$, gr2 $P=0.176$, gr3 $P=1$, gr4 $P=1$,
gr5 $P=1$,
gr6 $P=0.417$, gr7 $P=0.608$, gr11 $P=0.444$

Results: Temporal distribution of songs

Songs concentrated around dawn



Predictions

joint resource defense

songs more frequent / longer when:

- more fruits available ✓
- more resources needed,
e.g. pregnancy / lactation / ✓
bigger groups

songs concentrated around dawn ✓

songs longer during inter-group encounters ✓

mate defense (paternity guarding)

songs more frequent / longer when:

- females are receptive ✗

pair-bond reinforcement

songs produced all day ✗

songs not longer during ✗
inter-group encounters

Joint resource defense

Songs more frequent during pregnancy & lactation
(when more resources needed)



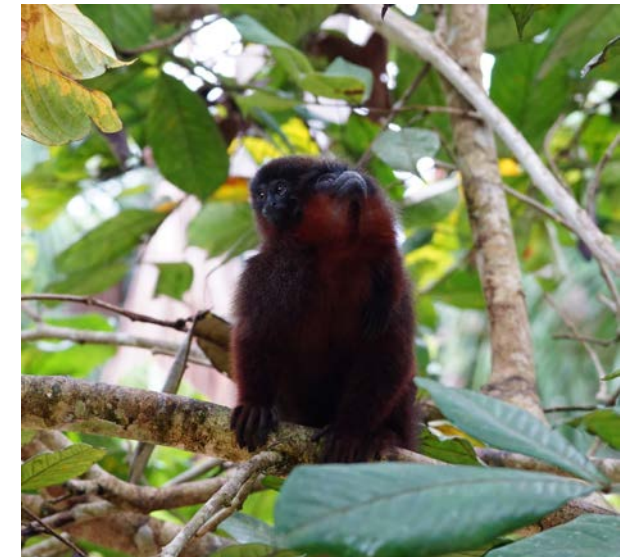
Méndez-Cárdenas
& Zimmermann
2009

Lactation is more energetically costly than pregnancy

Clutton-Brock et al., 1989; Altmann & Samuels
1992

Pregnant females consume more / better food

Dolotovskaya & Heymann 2020; Murray et al., 2009; Vasey,
2004, 2005



Titi monkeys:
infants carried by **males**

Open questions

Function of coordinated singing:

duets should be more effective than uncoordinated / solo songs

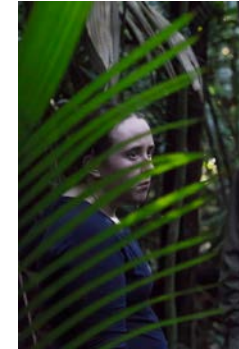
 playback studies

Resource defense

- duets more threatening than solos?
- when faced with intruders, partners duet?

Mate defense

- duets initiated by females?
- males join females more often when they are receptive ?



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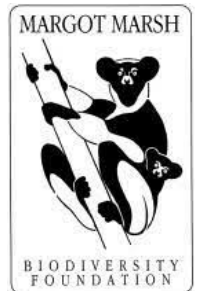
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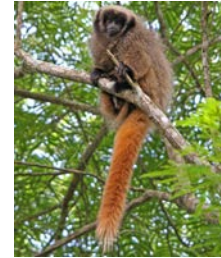
THE LEAKEY FOUNDATION



Mate defense

Songs least frequent when females are receptive

Caselli et al. 2014



Sex-specific spones to songs expected

Playback study in *Callicebus nigrifrons*:

- no sex-specific responses to duets / ♀ [solos] / ♂ [solos]
 - reactions to duets not stronger than to solos

Caselli et al. 2014

Pair-bond reinforcement

Songs concentrated around dawn => likely inter-group communication

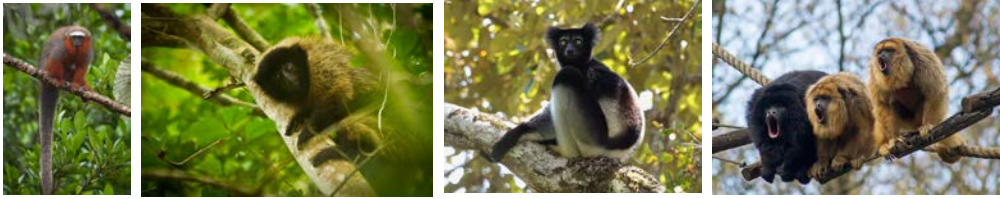
Lepilemur edwardsi dispersed pairs:
duets help coordinate activity



Méndez-Cárdenas
& Zimmermann
2009

Spatial distribution of songs

Songs throughout home range



Bonadonna et al. 2020; Van Belle et al. 2013, 2021; Martinez and Wallace 2017; Price & Piedade 2001; da Cunha & Byrne 2006

Songs at borders



Da Cunha & Jalles-Filho 2007

Related to home range size?



Kinzey & Robinson 1983

Joint resource defense

Songs slightly more frequent when more fruits are available

Caselli et al. 2014; Wright 2013, Cowlshaw 1996; Méndez-Cárdenas & Zimm...



Alternative explanation: songs are energetically costly

Cowlshaw 1996; Wich and Nunn 2002

Shorter daily path length during fruit scarcity

Nagy-Reis & Setz 2017; Wright 2013

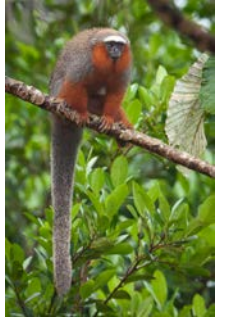


?

Energetic costs of singing compared to other activities

Open questions

- males more active in intergroup encounters
- captivity: males more “jealous” of same-sex intruders
- males more active in anti-predator behaviors



De Luna et al. 2010; Dolotovskaya et al. 2020; Lawrence 2007; Robinson 1981; Wright 1984



conflicting ♂ ♀ interests? division of labor?

Function of coordinated singing:
playback studies needed

Resource defense

- duets more threatening than solos?
- when faced with intruders, partners duet?

Mate defense

- duets initiated by females?
- males join females more often when they are receptive ?

higher fruit consumption in times of higher fruit availability was shown for black-fronted titi monkeys, *Callicebus nigrifrons* ([Caselli and Setz, 2011](#)), as well as other primates, e.g., *Hoolock hoolock* ([Neha et al., 2020](#)).

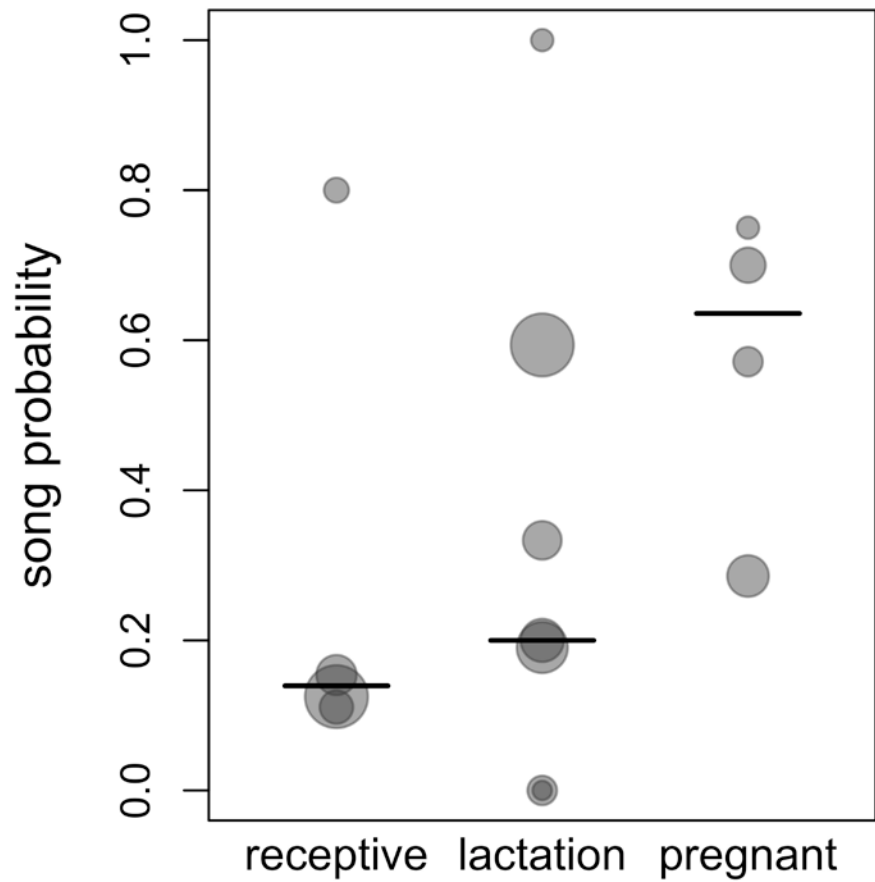


FIGURE 2. Song probability for different female reproductive states. Shown are proportions of singing days of all observation days, with each dot corresponding to one group ID and the area of the dots increasing linearly with the respective sample size for a given group and a given reproductive state (3 to 32 observation days per each combination of reproductive state and group ID, total $N = 171$ observation days). The lines depict the