

Twilight is for the nocturnal:

mammalian crepuscular activity is linked to nighttime activity

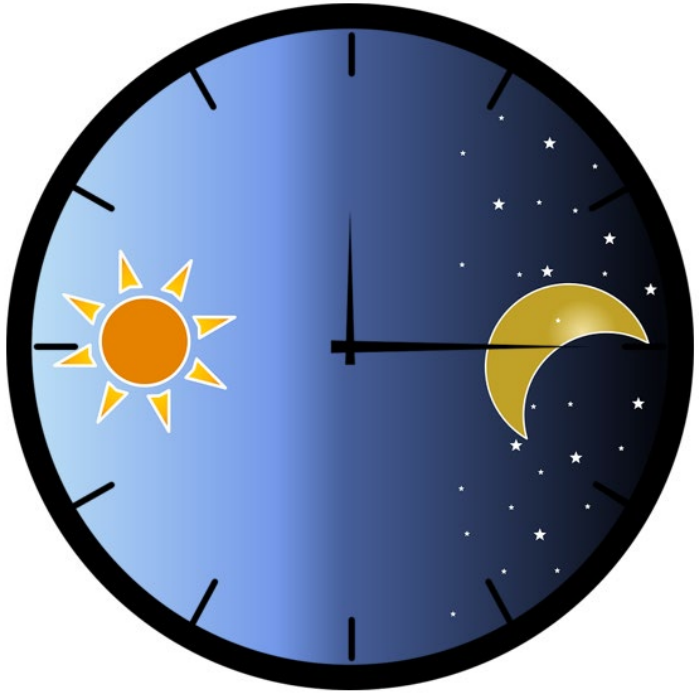
Brian D. Gerber[1], Kadambari Devarajan[2], Zach J. Farris[3], and Mason Fidino[4]

[1]USGS, Colorado Cooperative Research Unit, Colorado State University, USA
[2]Gobal Animal Diel Activity Project, Mumbai, India
[3]Appalachian State University, Boone, North Carolina, USA
[4]Conservation & Science Department, Lincoln Park Zoo, Chicago, Illinois, USA

Photo: Mike Pellinni

Animal Diel Ecology







Why study animal diel ecology?

- Fundamental to understand a species' niche

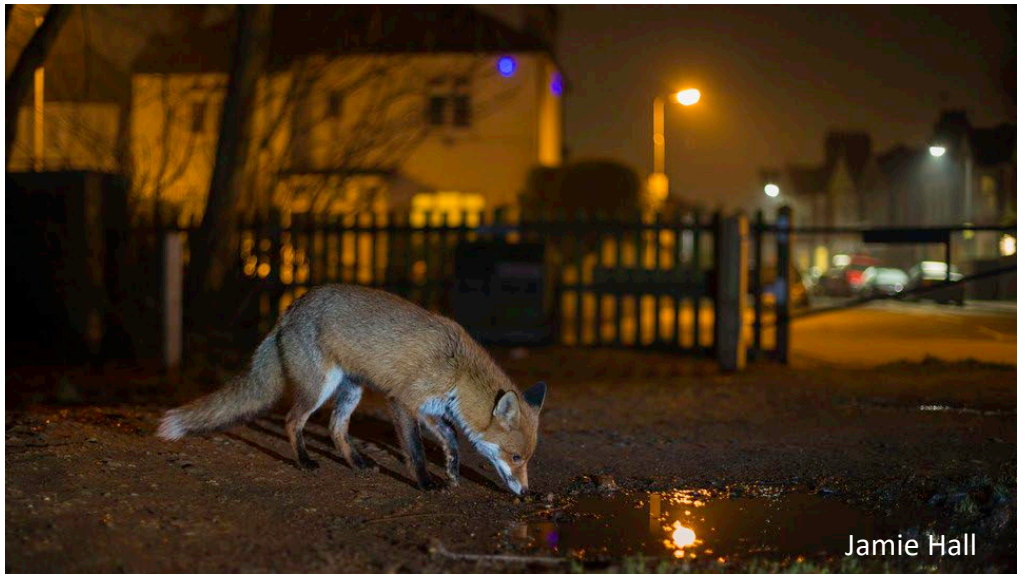




Pianka, 1973. Annual review of ecology and systematics, 53-74.
Enright, 1970. Annual review of ecology and systematics, 221-238.
Gaynor et al. 2018. Science. 1232-1235.
Rivera et al. 2022. Conservation Science and Practice: e13177

Why study animal diel ecology?

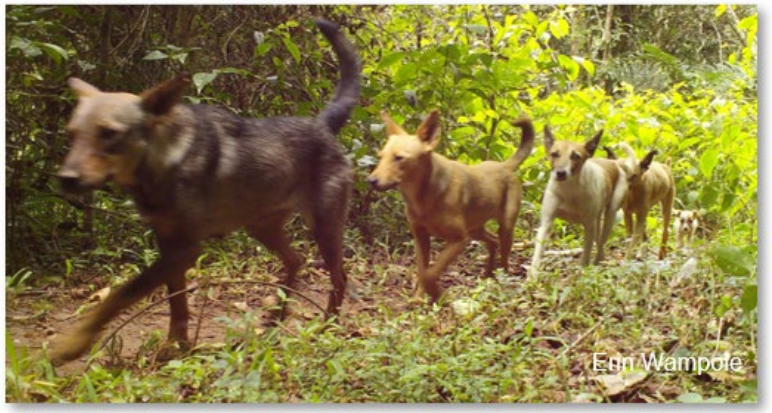
- Fundamental to understand a species' niche
- Diel behavior is a mechanism of adaptation to disturbance



Pianka, 1973. Annual review of ecology and systematics, 53-74.
Enright, 1970. Annual review of ecology and systematics, 221-238.
Gaynor et al. 2018. Science. 1232-1235.
Rivera et al. 2022. Conservation Science and Practice: e13177

Why study animal diel ecology?

- Fundamental to understand a species' niche
- Diel behavior is a mechanism of adaptation to disturbance
- Habitat requires resource to be present and accessible







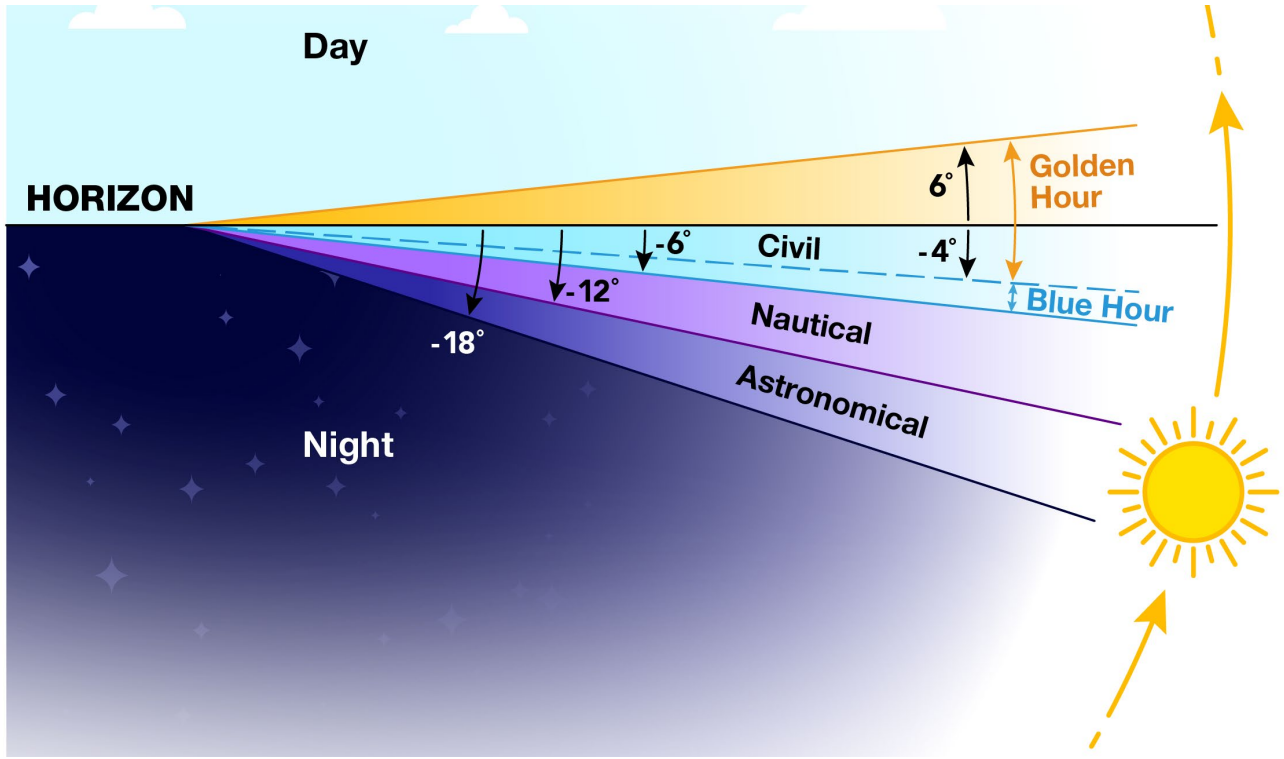
Pianka, 1973. Annual review of ecology and systematics, 53-74.
Enright, 1970. Annual review of ecology and systematics, 221-238.
Gaynor et al. 2018. Science. 1232-1235.
Rivera et al. 2022. Conservation Science and Practice: e13177

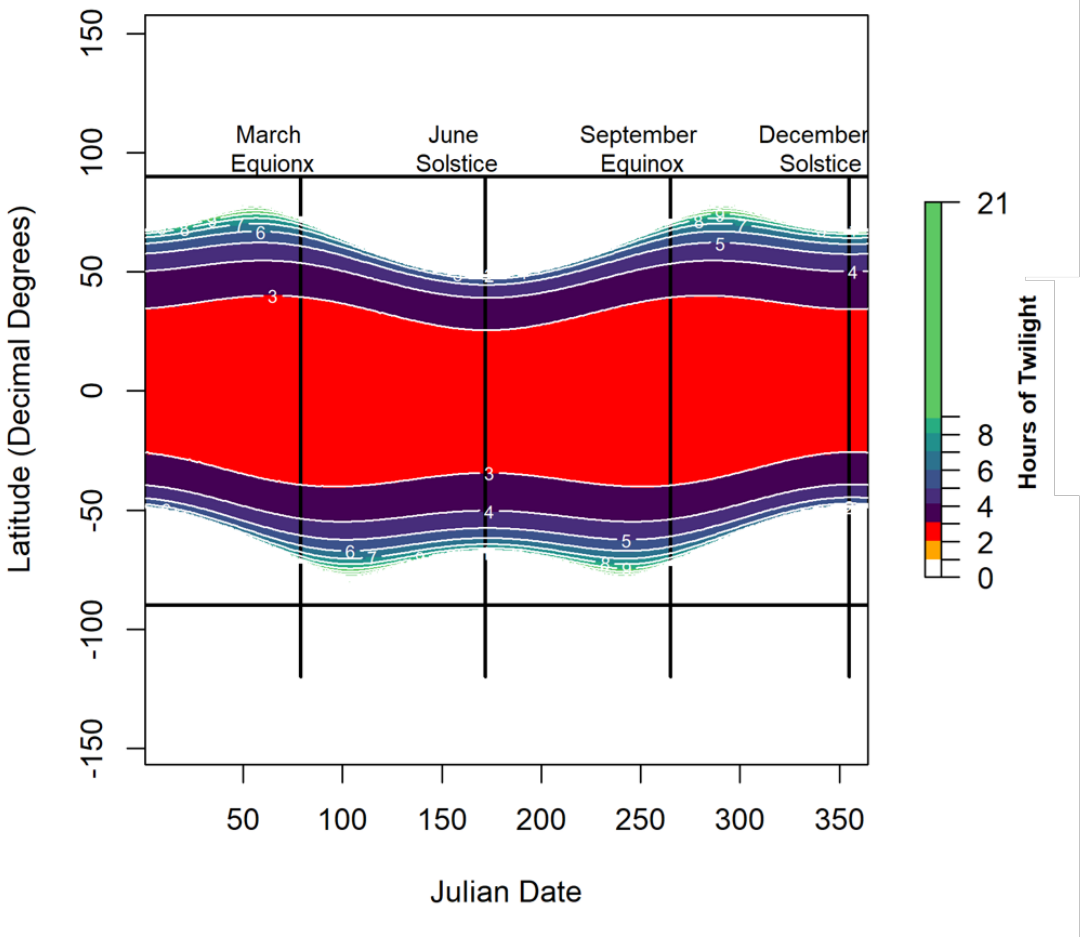
Diel Phenotypes / Chronotypes

- Diurnal: active during the daylight
- Nocturnal: active during the nighttime
- Crepuscular: active during twilight (i.e., dawn and dusk)
- Cathemeral: active throughout the 24-hr day

Schoener, T.W. 1974. Science, 185, 27-39.
Schoener, T.W. 1974. PNAS, 71, 4169-4172.
Kronfeld-Schor, N., & Dayan, T. 2003. Annual review of ecology, evolution, and systematics, 34, 153-181.
Anderson & Wiens. 2017. Evolution, 71, 1944-1959.
Levy et al. 2019. Ecological Monographs, 89, e01334.
Tattersall, I. 2006. Folia primatologica, 77, 7-14.

Twilight


Day
HORIZON
6°
Golden Hour
-4°
-6°
Civil
-12°
Nautical
-18°
Astronomical
Blue Hour
Night


March Equionx
June Solstice
September Equinox
December Solstice
Latitude (Decimal Degrees)
150
100
50
0
-50
-100
-150
50
100
150
200
250
300
350
Julian Date
Hours of Twilight
21
8
6
4
2
0

A crepuscular animal…

“has peaks during the twilight hours”

“is active primarily during the twilight period”

“is mainly active during twilight”

J. Vonk, T.K. Shackelford (eds.), Encyclopedia of Animal Cognition and Behavior,
https://en.wikipedia.org/wiki/Crepuscular_animal
Cox et al. (2024) *Trends in Ecology & Evolution* 39.1 31-40.

When the wild things are: Defining mammalian diel activity and plasticity

KADAMBARI DEVARAJAN, MASON FIDINO, ZACH J. FARRIS, SOLNY A. ADALSTEINSSON, GABRIEL ANDRADE-PONCE, JULIA L. ANGSTMANN, WHITNEY ANTHONYSAMY, JESICA AQUINO, ADDISU ASEFA, [...], AND BRIAN D. GERBER +207 authors Authors Info & Affiliations

SCIENCE ADVANCES • 26 Feb 2025 • Vol 11, Issue 9 • DOI: 10.1126/sciadv.ado3843

No support that species classified in the reference literature as crepuscular use mostly twilight (≥ 80%)

When the wild things are: Defining mammalian diel activity and plasticity

KADAMBARI DEVARAJAN, MASON FIDINO, ZACH J. FARRIS, SOLNY A. ADALSTEINSSON, GABRIEL ANDRADE-PONCE, JULIA L. ANGSTMANN, WHITNEY ANTHONYSAMY, JESICA AQUINO, ADDISU ASEFA, [...], AND BRIAN D. GERBER +207 authors Authors Info & Affiliations

SCIENCE ADVANCES • 26 Feb 2025 • Vol 11, Issue 9 • DOI: 10.1126/sciadv.ado3843

No evidence that any species
(n = 445) used twilight (≥80%)

When the wild things are: Defining mammalian diel activity and plasticity

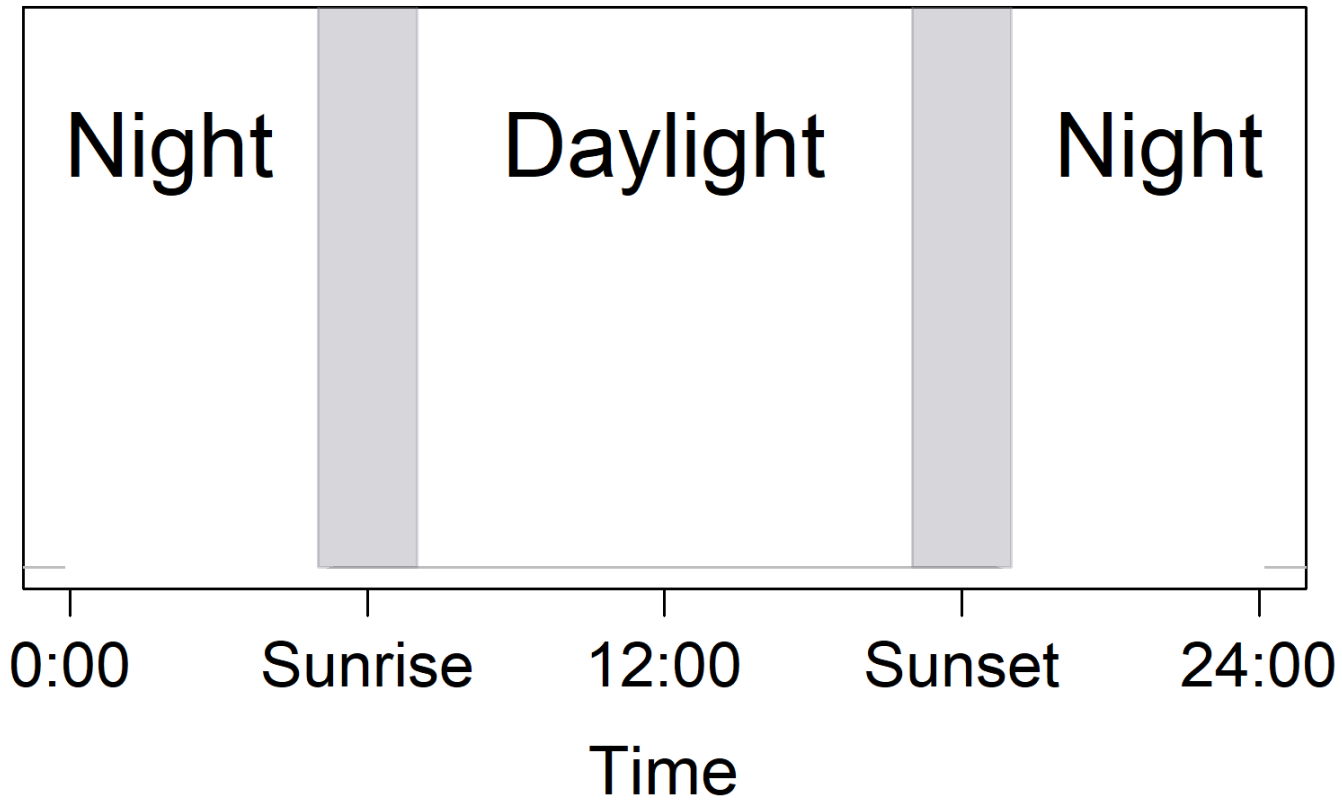
KADAMBARI DEVARAJAN, MASON FIDINO, ZACH J. FARRIS, SOLNY A. ADALSTEINSSON, GABRIEL ANDRADE-PONCE, JULIA L. ANGSTMANN, WHITNEY ANTHONYSAMY, JESICA AQUINO, ADDISU ASEFA, [...], AND BRIAN D. GERBER +207 authors Authors Info & Affiliations

SCIENCE ADVANCES • 26 Feb 2025 • Vol 11, Issue 9 • DOI: 10.1126/sciadv.ado3843

Only 5 (n = 14,587) diel classification estimates supported that ≥ 50% occurred during twilight.

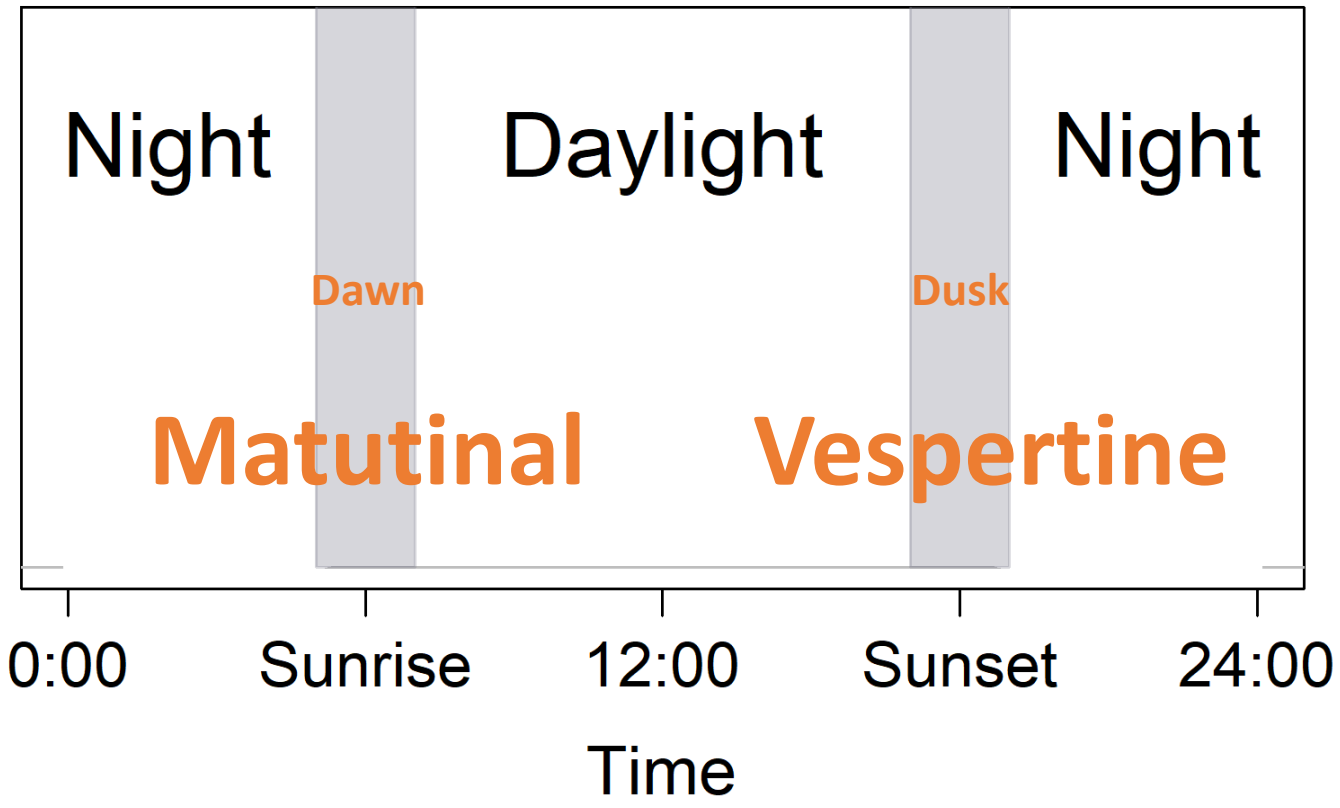
Selection, not use

Account for available time within each diel period to estimate diel selection



Bischof et al. 2024 PRSB, 291.2033
Gallo et al 2022. Elife, 11, e74756

Dawn is not dusk; dusk is not dawn

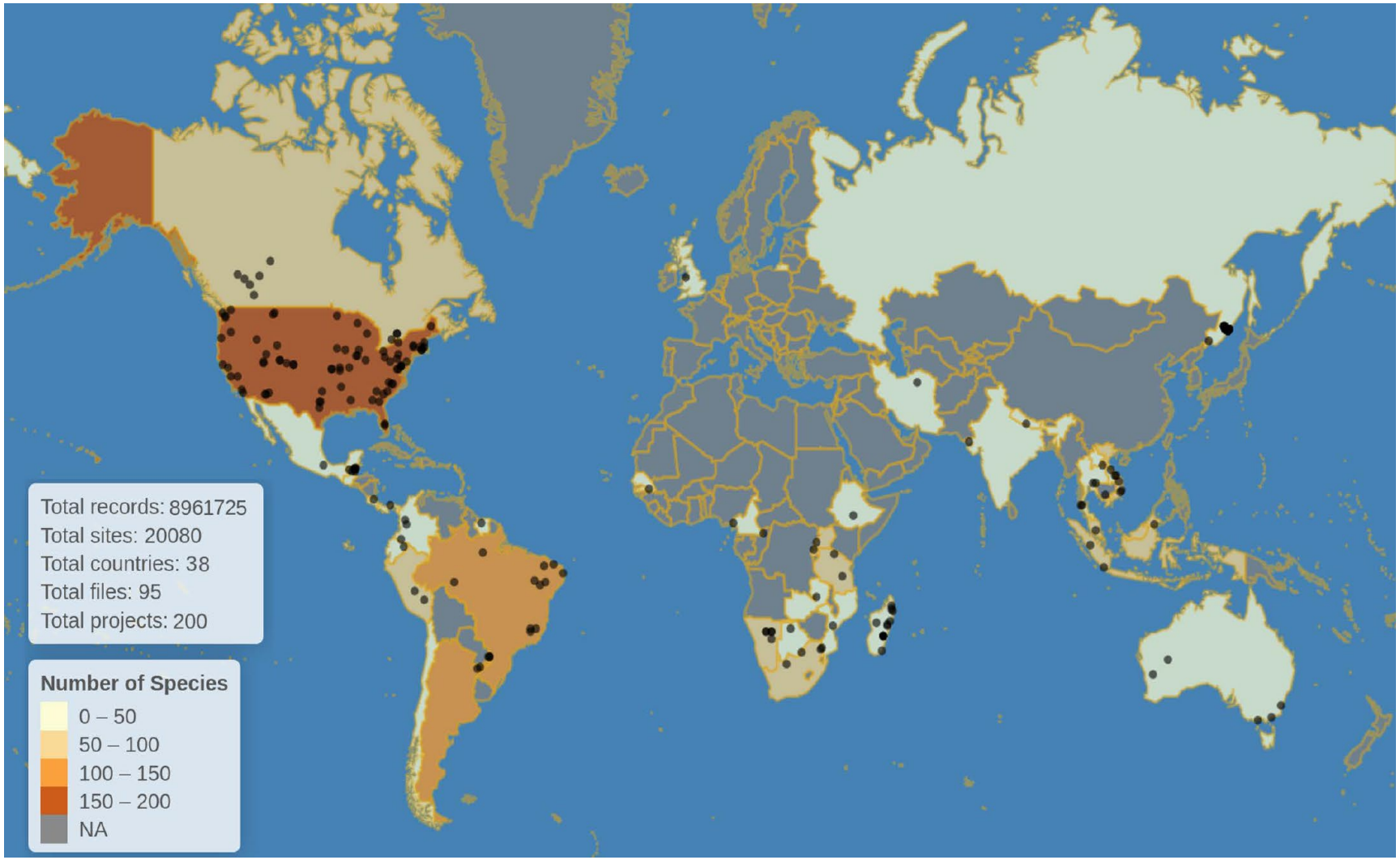


Objectives

Evaluate whether mammal species are ‘crepuscular’, in terms of separate selection of dawn and dusk

- Is this a rare behavior?
- Is crepuscular selection a unique chronotype or is it tied to selection of daytime/nighttime selection?

Data



38 Countries

392 Species

~9 million records

14,053 unique spatio-temporal analysis units

Devarajan et al. 2025. Science Advances. 11.9: eado3843.

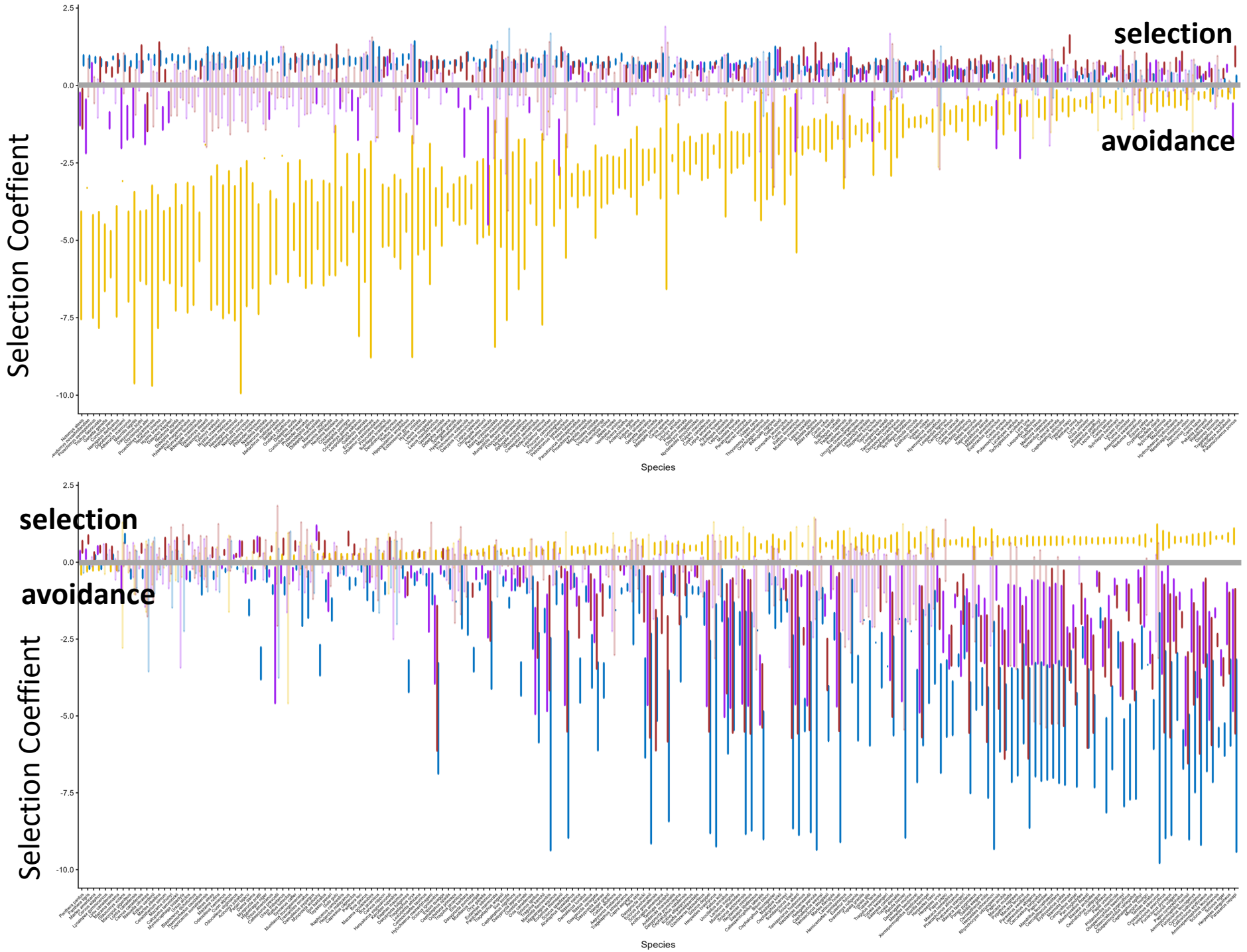
Statistical Model

Bayesian Hierarchical Poisson Regression / Temporal Selection

- available time in a diel period via an offset
- selection parameters nested within species nested within family
- additional analysis unit- and project-level variance
- Priors were diffuse to conservative towards no selection/avoidance

Model Fit

- $\hat{R}$<1.1
- Bayesian p-value to assess goodness of fit ~ 0.5


selection
avoidance
Selection Coeffient
2.5
0.0
-2.5
-5.0
-7.5
-10.0
Species
selection
avoidance
Selection Coeffient
2.5
0.0
-2.5
-5.0
-7.5
-10.0
Species
Dawn
Daytime
Dusk
Night

Results

Is this a rare behavior?

- 46 species (12%) selected for both dawn and dusk, separately (crepuscular)
- 81 species (21%) selecting dusk, but not dawn (vespertine)
- 9 species (2%) selecting dawn but not dusk (matutinal)

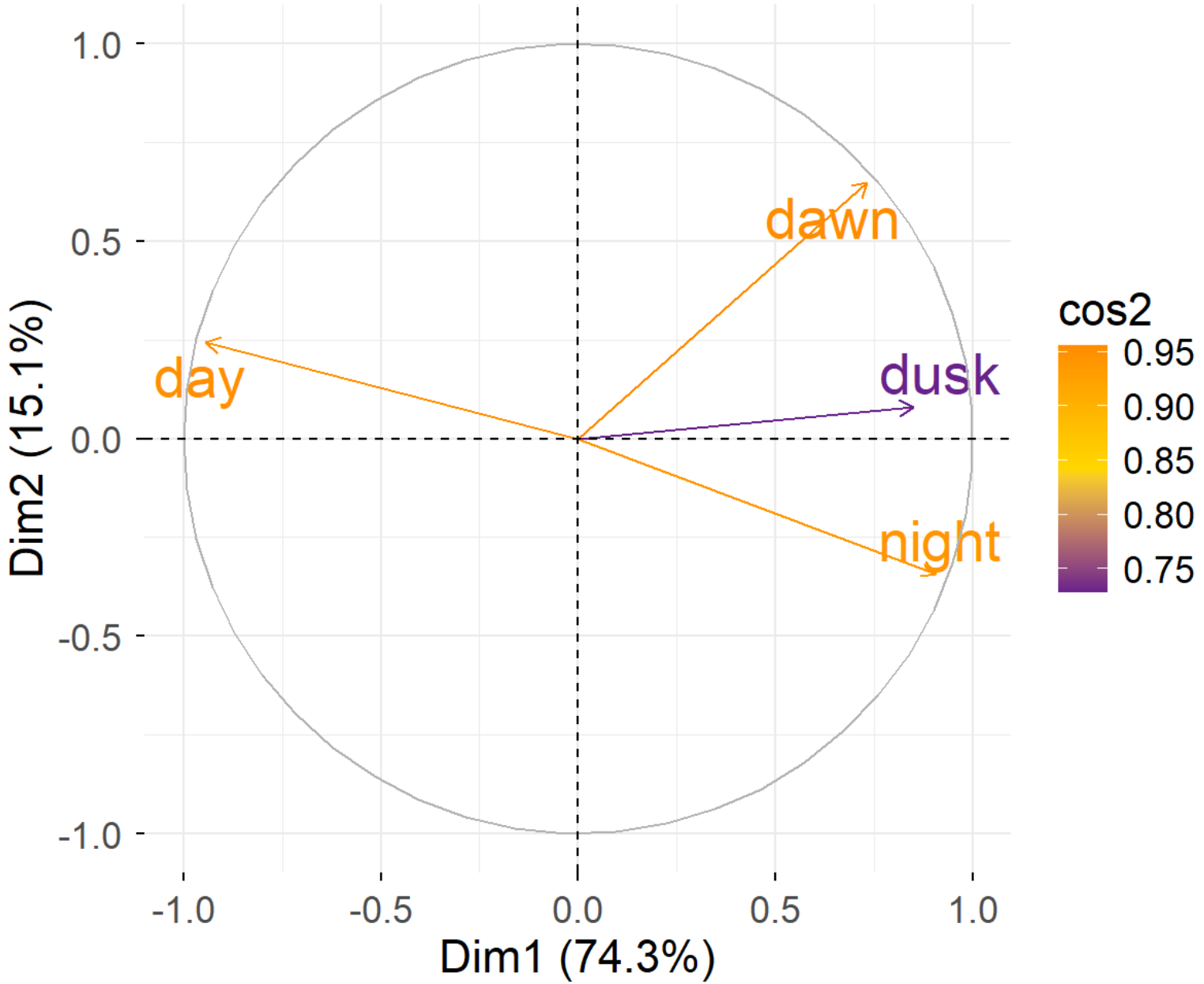
Results

Is crepuscular selection a unique chronotype?

- No species selected dawn and dusk, while avoiding day and night

- Of the 137 species selecting for daytime, 99% avoided nighttime
  - 0% selected dawn and 64% avoided dawn
  - 7% selected dusk and 54% avoided dusk

- Of the 172 species selecting for nighttime, 100% avoided daytime
  - 23% selected dawn and 17% avoided dawn
  - 52% selected dusk and 1% avoided dusk


1.0
0.5
0.0
-0.5
-1.0
Dim2 (15.1%)
-1.0
-0.5
0.0
0.5
1.0
Dim1 (74.3%)
dawn
day
dusk
night
cos2
0.95
0.90
0.85
0.80
0.75

‘Crepuscular’ is not a distinct diel phenotype

- Species that select for twilight (dawn and/or dusk) do not do so exclusively and in contrast to avoiding other periods
- Species that select for dawn or dusk also tend to select for nighttime and avoid daytime
- No species “primarily” use twilight (Devarajan et al. 2025)
- The functional trait space of ‘nocturnal’ and ‘crepuscular’ completely overlap (Cox et al. 2021)
- No morphological distinction b/w crepuscular and cathemeral species (Schmitz and Motani, 2010; Hall et al. 2012)

Diel phenotype hypotheses for use or selection

- Diurnal: active during the daylight
- Nocturnal: active during the nighttime
- Cathemeral: active throughout the 24-hr day

Thank you to 215 collaborators….

Adalsteinsson, SA, Andrade-Ponce, G, Angstmann, JL, Anthonysamy, W, Aquino, J, Asefu, A, Avila, B, Bailey, LL, de Sousa, LM, de Frias Barreto, BM, Bartlow, K, Barton, O, Bates, CE, Guimarães Beltrão, M, Bird, T, Biro, EG, Bisi, F, Bohórquez, D, Boyce, M, Brashares, JS, Bullington, G, Burns, P, Burr, J, Butler, AR, Calhoun, KL, Trung Cao, T, Casado, N, Cepeda-Duque, JC, Cepek, JD, Garcia Chiarello, A, Collins, M, Cordeiro-Estrela, P, Costa, S, Cremonesi, G, Cristescu, B, Cruz, P, de Albuquerque, ACF, De Angelo, C, de Campos, CB, de Sena, LMM, Di Bitetti, M, de Matos Dias, D, Diefenbach, D, Doherty, TS, dos Santos, TP, Teixeira Duarte, G, Eppley, TM, Erb, J, Franco Esteves, C, Evans, B, Falcão, MLM, Fernandes-Ferreira, H, Fieberg, JR, de Souza Filho, LCF, Fisher, J, Fortin, M-J, Gale, GA, Gallo, T, Ganoe, LS, Garcia-Anleu, R, Gaynor, KM, Gelmi-Candusso, TA, Gichuru, PN, Gomez, Q, Green, AM, Neves Guimarães, L, Haight, JD, Harris, LR, Hawn, ZD, Heiman, J, Quoc Hoang, H, Huebner, S, Iannarilli, F, Eugenia Iezzi, M, Ivan, JS, Jaspers, KJ, Jordan, MJ, Kamilar, J, Kane, M, Karimi, MH, Kelly, M, Kohl, MT, Kuvlesky, WP, Ladle, A, Larson, RN, Tan Le, Q, Le, D, Son Le, V, Lehrer, EW, Lendrum, PE, Lewis, J, Link, A, Lizcano, DJ, Lombardi, JV, Long, R, López-Tello, E, Lugarini, C, Lugo, D, MacKay, P, Madadi, M, Magalhães, RA, Magle, SB, Mandujano, S, Marchenkova, T, Henrique Marinho, P, Marker, L, Martinez Pardo, J, Martinoli, A, Massara, RL, Masseloux, J, Matiukhina, D, Mayer, A, Mazariegos, L, McBride, A, McClung, MR, McInturff, A, McPhail, D, Mertl, A, Middaugh, CR, Miller, D, Mills, D, Miquelle, D, Miritis, V, Moll, RJ, Molnár, P, Montgomery, RA, Morelli, TL, Mortelliti, A, Muelle, RI, Mukhacheva, AS, Mullen, K, Murphy, A, Nepomuceno, V, Ngoprasert, D, Nguyen, A, Van Nguyen, T, Van Nguyen, T, Anh Nguyen Quang, H, Nipko, R, Nobre, ACC, Northrup, J, Owen, MA, Paglia, AP, Palmer, MS, Palomo-Munoz, G, Pardo, LE, Parks, C, de Oliveira Paschoal, AM, Patterson, B, Paviolo, A, Pejchar, L, Pendergast, ME, Perotto-Baldivieso, HL, Petrov, T, Poisson, MKP, Polli, DJ, Pourmirzai, M, Reebin, A, Remine, KR, Rich, L, Richardson, CS, Robino, F, Rocha, DG, Rocha, FL, Rodrigues, F, Rohnke, AT, Ryan, TJ, Salsbury, CM, Sander, HA, da Cruz Santos- Cavalcante, NM, Sekercioglu, CH, Seryodkin, I, Setiawan, DH, Shadloo, S, Shahhosseini, M, Shannon, G, Shier, CJ, Smith, GB, Snyder, T, Sollmann, R, Sparks, KL, Sribuarod, K, St Clair, CC, Stankowich, T, Steinmetz, R, Stevenson, CJ, Sunarto, Surasinghe, TD, Sutyrina, SV, Swaisgood, RR, Taktehrani, A, Thapa, K, Thorton, M, Tilker, A, Tobler, MW, Van Bang, T, Tucker, J, Van Horn, RC, Vargas-Soto, JS, Velásquez-C, KL, Venter, J, Venticinque, EM, Verschueren, S, Wampole, E, Watchorn, D, Wearn, OR, Weiss, KC, Welschen, A, Widodo, FA, Williamson, J, Wilting, A, Wittemeyer, G, Zavaleta, A, Zellmer, AJ