



Ptačí ekologie: temperátní vs. globální měřítko

Jak budeme přepisovat učebnice?

Tomáš Grim, Katedra zoologie, UP Olomouc



Doporučená literatura



Doporučená literatura

- Terborgh J. et al. 1990: Structure and organization of an amazonian forest bird community. Ecol. Monogr. 60: 213-238.
- Martin T. E. 1996: Life history evolution in tropical and south temperate birds: What do we really know? J. Avian Biol. 27: 263-272.
- Martin T. E. 2004: Avian life-history evolution has an eminent past: does it have a bright future? Auk 121(2): 289-301.
- Martin T. E. et al. 2000: Parental care and clutch sizes in North and South American birds. Science 287: 1482-1485.
- Martin T. E. 2008: Egg size variation among tropical and temperate songbirds: An embryonic temperature hypothesis. Proc. Natl. Acad. Sci. USA 105: 9268-9271.
- Schaefer H. C. et al. 2004: Life-history of two African *Sylvia* warblers: low annual fecundity and long post-fledging care. Ibis 146(3): 427-437.
- Slater P. J. B. & Mann N. I. 2004: Why do the females of many bird species sing in the tropics? J. Avian Biol. 35(4): 289-294.



... i český článek (sic!)



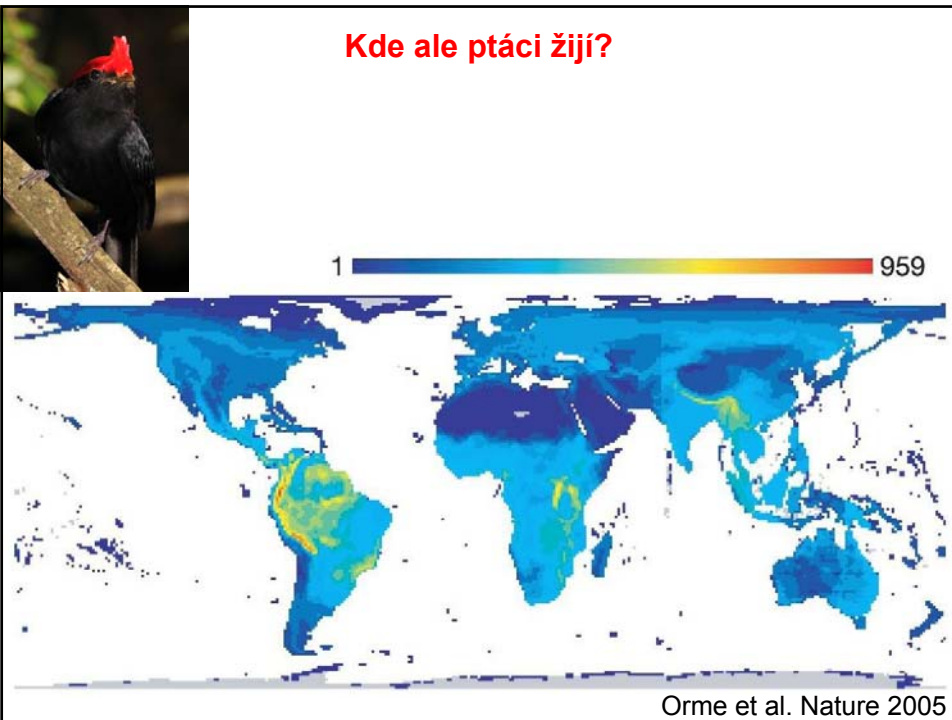
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Význam studia ptáků pro biologii obecně

- „ekologie chování = ekologie chování ptáků“ (ekologie, evoluce, ...)
- *Agelaius phoeniceus*, *Parus major*, *Hirundo rustica*
- model: ptáci mírného pásu



Kde ale ptáci žijí?



Tropičtí ptáci se ale studují také – modely divného chování

• **bizarní biologie** některých ptáků tropických:

- cooperative breeders
- lekking
- ant-following
- mixed-species flocks
- duetting etc.



Guira guira

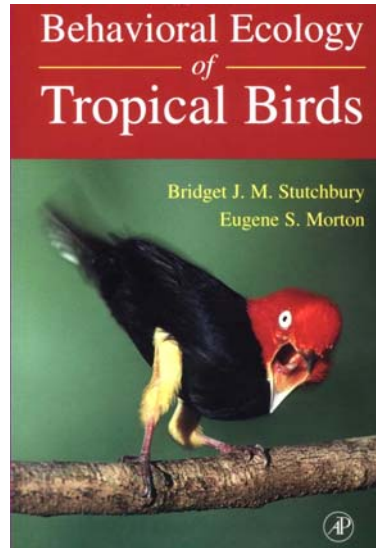
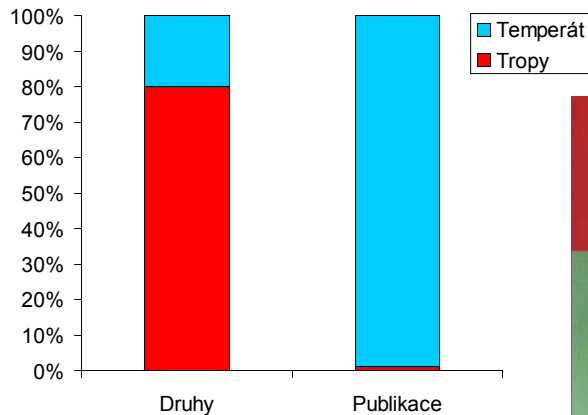
• ... ale co ti „normální“ obyčejní tropičtí ptáci?



Typičtí tropičtí ptáci jsou však také úplně jiní!

	mírný pás	tropy
velikost snůšky	4 – 6	2
velikost vejce	malá	velká
počet snůšek/rok	1 – 2	4 – 5
hnízdni období	3 – 4 měsíce	6 – 10 měsíců
inkubace	♀	♂ + ♀
krmení mláďat	♀ > ♂	♂ + ♀
frekvence krmení	vysoká	nízká
délka rodičovské péče	krátká	dlouhá
zpěv	♂	♂ + ♀
zpívají	hodně	velice málo
zpěvní aktivita	v hnízdním období	celoročně
EPC	běžné	vzácné
hladina testosteronu	proměnlivá, vysoká	trvale nízká

Temperate Zone Bias – vadí to?



Vadí to hodně! Proč?

- učebnicové generalizace stojí na vodě
- tradiční modelové druhy můžou být úchylné – nereprezentativnost
- nedostatečná variabilita v zkoumaných znacích

! Given that north-temperate species represent a minor proportion of the species of the world with life histories that deviate from the majority of species of the world, we need to ask: Are north-temperate species the appropriate models for understanding avian life-history evolution in general?

„Proč jsou tropičtí ptáci jiní?“



„Proč jsou ptáci mírného pásu tak atypičtí?“

Jaké jsou rozdíly ...

chronologicky:

- potrava a specializace
- teritorialita a testosteron
- velikost snůšky
- velikost vejce
- inkubační perioda

Potrava a specializace

Potravní specializace

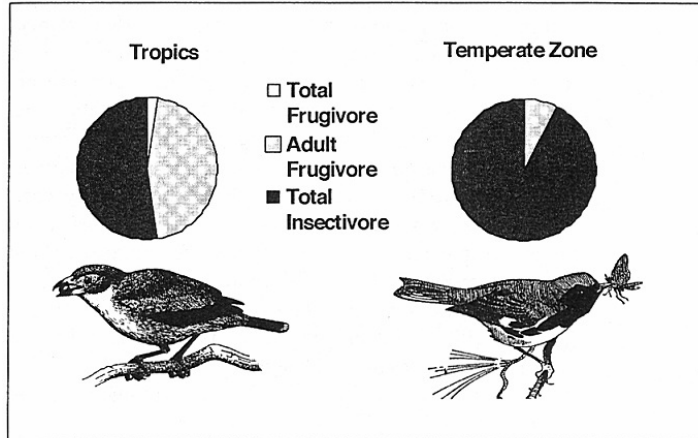


Figure 7.2

Proportion of passerine genera that are total frugivores (adults and nestlings eat fruit), adult frugivores (adults eat fruit, nestlings eat insects), and total insectivores (adults and nestlings eat insects) in Panama ($n = 204$ genera) and North America ($n = 94$ genera). Drawings of temperate Black-throated Blue Warbler from Griscom and Sprunt (1957) and tropical Masked Tityra from Wetmore (1972).

Potravní specializace

Potravní zdroje a strategie:

- plody (Pipridae, Trogonidae, Psittacidae)
- ant-following (Formicariidae, Dendrocolaptidae)
- sledování opic (*Harpagus bidentatus*, *Monasa nigrifrons*)
- sledování pekariů (*Neomorphus* spp.)
- suché listy (*Sclerurus*, *Cacicus melanicterus*)
- liány (*Ramphocaenus melanurus*)
- nektar, nezralé plody, olbřímí hmyz, epifyty ...



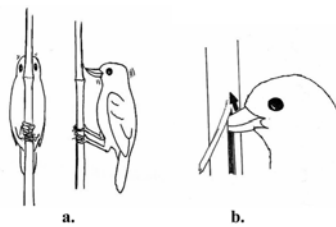
➤ ... vysvětlují 1/3 nárůstu ptačí diverzity v tropech



Potravní specializace

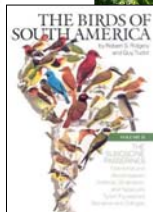


Clytoctantes alixii



Biotopová specializace

- palmová savana – moriche (*Mauritia flexuosa*)
- *Berlepschia rikeri*
- *Tyrannopsis sulphurea*
- *Icterus chryscephalus*
- *Tachornis squamata*



Velikost teritoria: páry a hektary

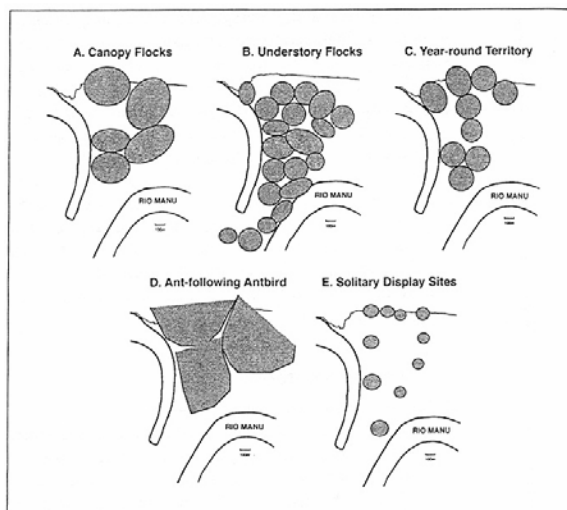


Figure 5.1

Representative territory types in a floodplain forest in Amazonian Peru (Terborgh et al. 1990). Shaded areas are territories.

Terborgh et al. Ecol. Monogr. 1990

Velikost teritoria

TABLE 1. Mean territory sizes and body masses for some avian guilds in mature Amazonian floodplain forest.*

Guild	N	Mean territory size (ha)	Mean body size (g)*
Insectivore	83	14	50
Arboreal			
Gleaning	24	8	23
Sallying	30	12	54
Bark			
Interior	4	43	160
Surface	6	16	45
Terrestrial	9	13	51
Omnivore	16	12	50

Terborgh et al. Ecol. Monogr. 1990

Proč toho víme o tropických ptácích málo?

Jsou těžko detekovatelní



The Wilson Journal of Ornithology 118(1):109–112, 2006

A New Record of the Endangered White-winged Nightjar (*Eleothreptus candicans*) from Beni, Bolivia

Tomáš Grim,^{1,3} and Radim Šumbera²

Žijí velice skrytě



Nejdou poznat



HBW Vol. 9 2004

Zpívají málo a nenápadně



Pipreola arcuata

Často nevíme, že koukáme na něco zajímavého!



©Cacomantis, MARKchua



Cacomantis©MARKchua

The Wilson Journal of Ornithology 120(4):887–890, 2008

Begging Behavior of Fledgling Rusty-breasted Cuckoo
(*Cacomantis sepulcralis*)

Tomáš Grim¹

Grim J. Ethol. 2008

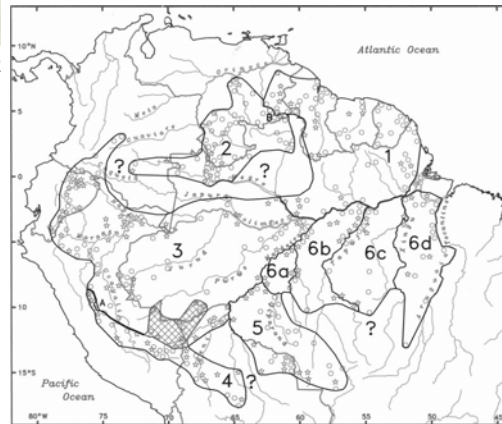
Často nevíme, co to je vůbec za taxon!



Hypocnemis subflava & *H. peruviana*

Hypocnemis

- 1 = *cantator*
- 2 = *flavescens*
- 3 = *peruviana*
- 4 = *subflava*
- 5 = *ochrogyna*
- 6a = *taxon novum*
- 6b = *implicata*
- 6c = *striata*
- 6d = *affinis*



Isler et al. Auk 2007

Teritorialita a testosteron

Potravní nabídka

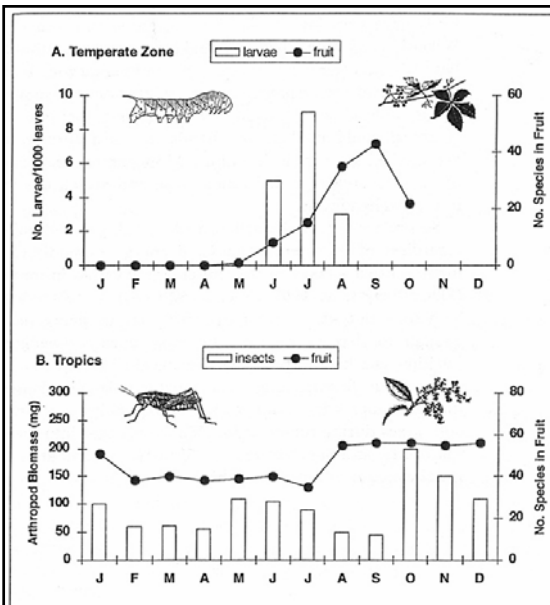


Figure 7.1

Insect and fruit abundance over the year in the temperate zone versus tropics. Caterpillar data from New Hampshire (Holmes et al. 1986) and arthropod data (biomass per 30 sweeps) from Costa Rica (Young 1994). Fruiting data from Illinois (Thompson and Willson 1979) and Costa Rica (Levey 1988).

Délka hnízdního období

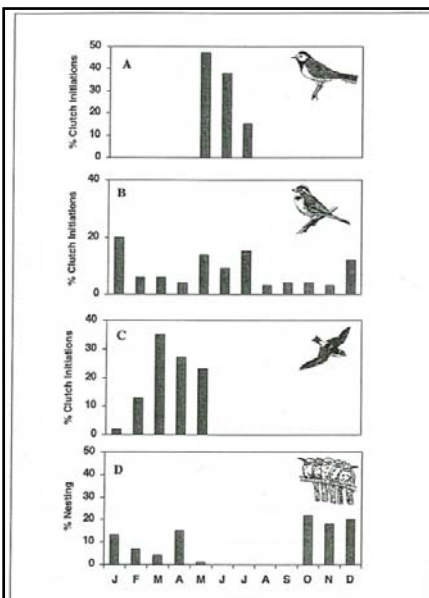


Figure 2.1

Breeding season length for A) Typical temperate zone passerine, the Hooded Warbler, *Wilsonia citrina* (Evans Ogden and Stutchbury 1996) B) Rufous-collared Sparrow, *Zonotrichia capensis* (Miller 1962), C) Mangrove Swallow, *Tachycineta albilinea* (Moore et al. 1999) and D) White-fronted Bee-eater, *Merops bullockoides* (Wrege and Emlen 1991). Drawings from Owings and Morton (1998), Wetmore (1984), and Krebs and Davies (1991).



Chování: zpěvná aktivita

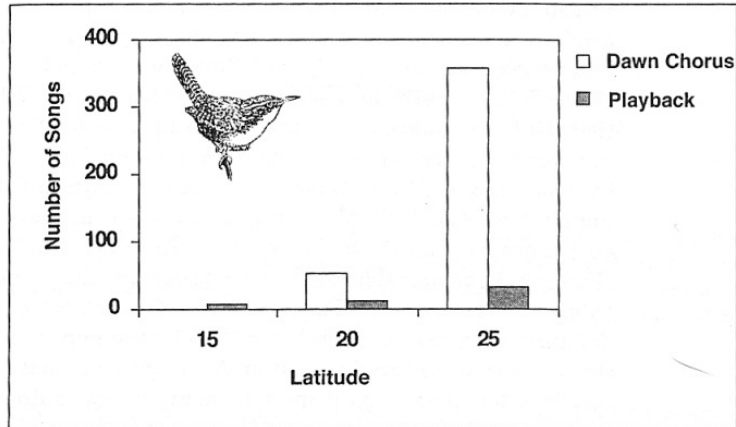


Figure 6.4

Song rate of male Carolina Wrens outside of the breeding season at different latitudes. Shown are the number of songs given per hour during the dawn chorus, and the total number of songs given after stimulus by a playback of conspecific song within the male's territory (data from Morton 1982). Drawing from Owings and Morton (1998).

Fyziologie: teritorialita a testosteron

testosteron vs. imunita (vs. energetické výdaje)

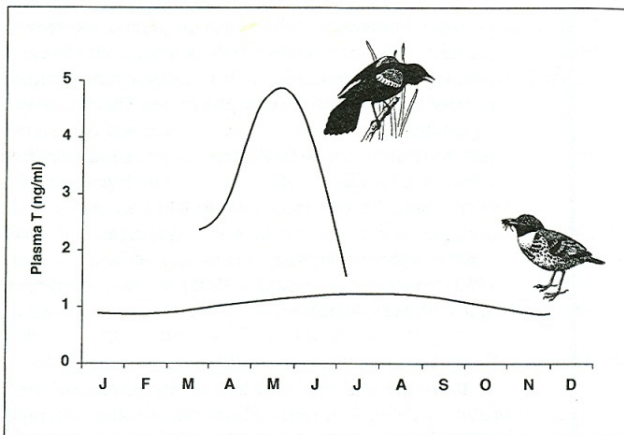


Figure 5.2

Plasma testosterone level (ng ml^{-1}) of male **Spotted Antbirds** in Panama over the year, including the breeding season from April–November (from Wikelski *et al.* 1999a), and for **Red-winged Blackbirds** in North America that breed from April–June (Johnsen 1998). Drawings from Medsger (1931) and Wetmore (1972).



Anatomie: velikost varlat

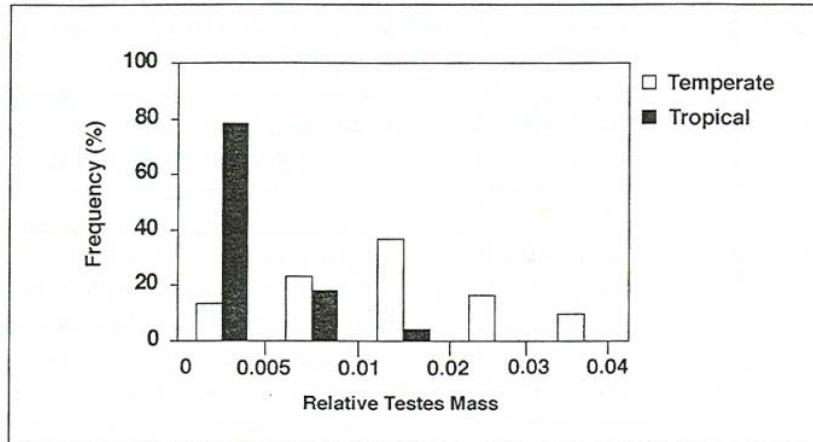


Figure 4.1

Testes mass (relative to body mass) of Neotropical passerines and North American temperate migrants (data from Stutchbury and Morton 1995).

ale viz Calhim & Birkhead Behav. Ecol. 2007

EPY



TABLE 1. Frequency of extra-pair fertilizations and extent of breeding synchrony in socially monogamous tropical passerines. Values give % of extra-pair young and broods that contained at least one extra-pair young (sample size in parentheses), and the breeding synchrony index (Kempnaers 1993).

Species	EPF frequency, %		Breeding synchrony (%)
	Young	Broods	
<i>Cercomacra tyrannina</i> ^a	0 (15)	0 (12)	8
<i>Tachycineta albilinea</i> ^b	15 (98)	26 (30)	8
<i>Elaenia flavogaster</i> ^c	4 (24)	8 (13)	9–10
<i>Thryothorus leucotis</i> ^d	4 (53)	3 (31)	10
<i>Zosterops lateralis</i> ^e	0 (122)	0	12
<i>Loxioides bailleui</i> ^f	0 (20)	0 (12)	low
<i>Geospiza scandens</i> ^g	8 (159)	15 (66)	low
<i>Elaenia chiriquensis</i> ^h	37 (14)	67 (15)	15–18
<i>Turdus grayi</i> ⁱ	38 (37)	53 (19)	25
<i>Volatinia jacarina</i> ^j	50 (20)	64 (7)	30

Macedo et al. Auk 2008

vs.

Stutchbury & Morton Wilson J. Ornithol. 2008

Synchronizace hnízdění vs. EPC

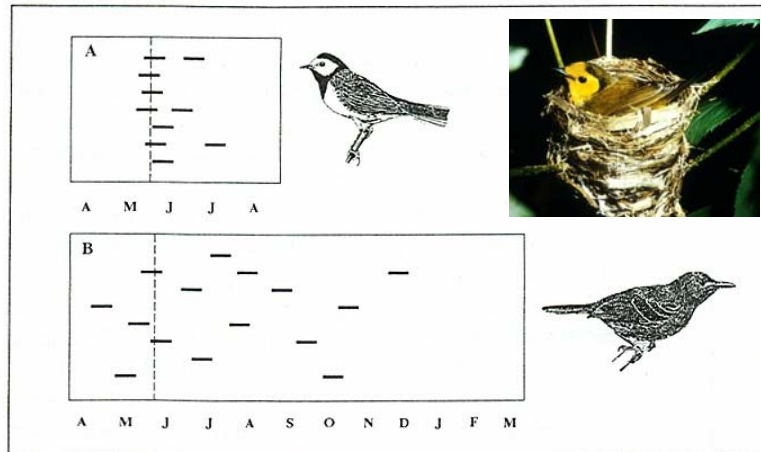


Figure 4.3

Temporal distribution of female fertile periods (solid bars) in A) a typical synchronously breeding temperate bird, the Hooded Warbler and B) a typical asynchronously breeding tropical bird, the Dusky Antbird. Dashed lines illustrate the difference in breeding synchrony. Drawings from Owings and Morton (1998) and Haverschmidt (1968).

Zpětnovazebná evoluce divergence pohlavních rolí?

časově omezená potravní nabídka v mírném pásu

⓪

synchronizace hnízdění

⓪

EPC

⓪

vysoký testosteron

⓪

nízká jistota otcovství

⓪

redukce otcovské péče

⓪

divergence pohlavních rolí



Stutchbury & Morton Behaviour 1995

Teritorialita a zpěv

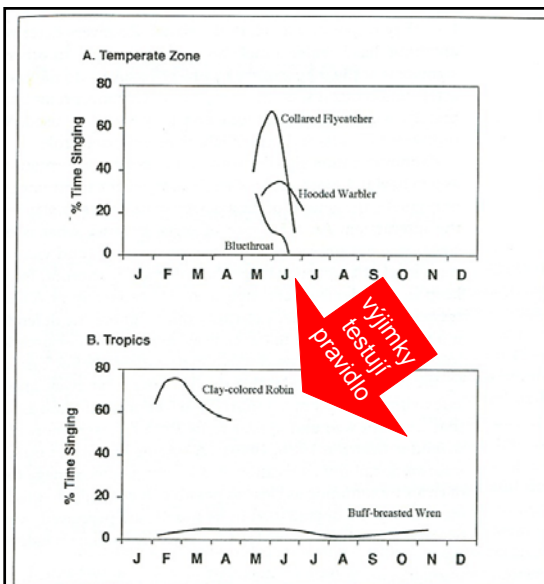


Figure 6.1

Song output (% time singing) versus time of year for A) typical temperate zone passerines the Collared Flycatcher *Ficedula albicollis* (Pärt 1991), Bluetthroat *Luscinia svecica* (Kroene et al. 1996) and Hooded Warbler (Wiley et al. 1994) and B) the tropical Clay-colored Robin (Stutchbury et al. 1998) and Buff-breasted Wren (S. Gill, unpubl).



Velikost snůšky

Velikost snůšky = 1 vejce!



Buarremon brunneinuchus (*Atlapetes brunneinucha*)

Latitudinální gradient velikosti snůšky

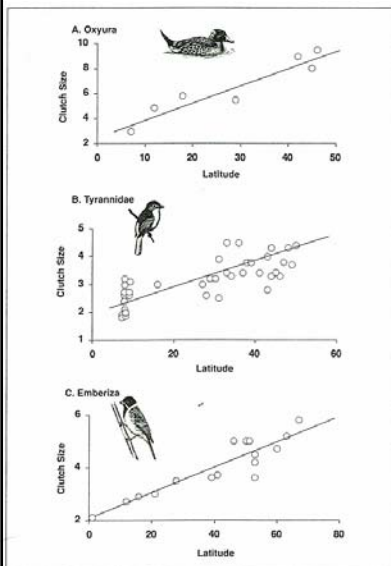
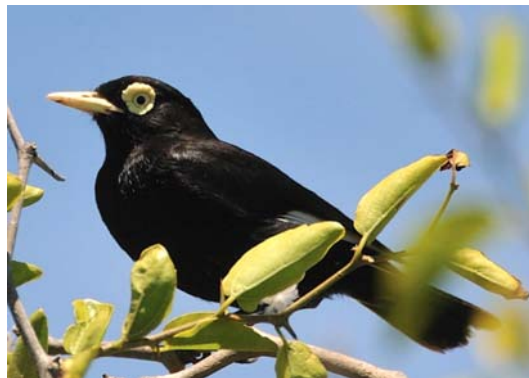


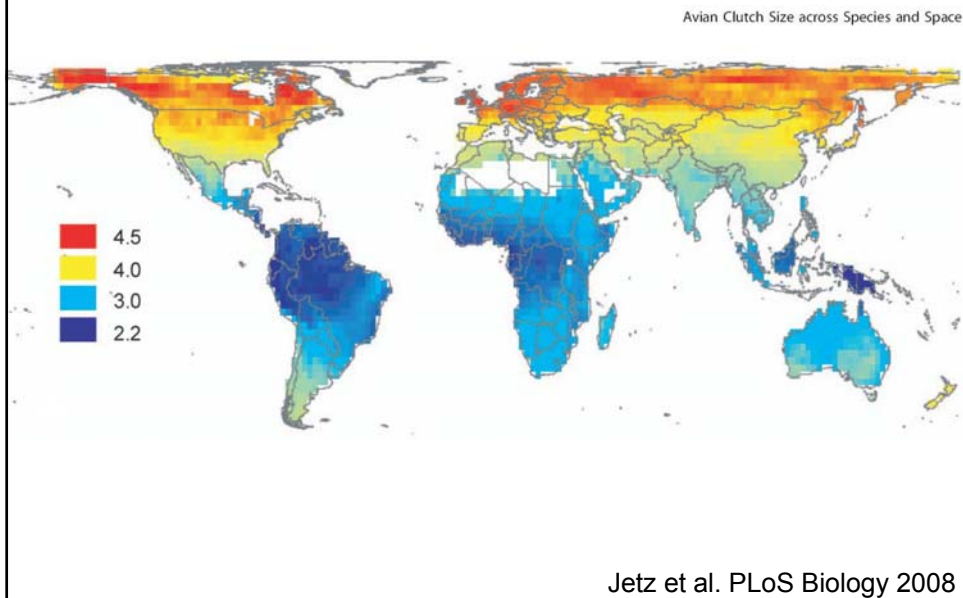
Figure 3.3

Clutch size versus latitude for A) the genus *Oxyura* (stiff-tailed ducks), worldwide B) the family Tyrannidae (flycatchers), Central and North America C) the genus *Emberiza* (sparrows, finches), Africa, Europe and Asia. Data from Cody (1966). Drawings from Sick (1993), Skutch (1997), and Etchebar and Hue (1997).

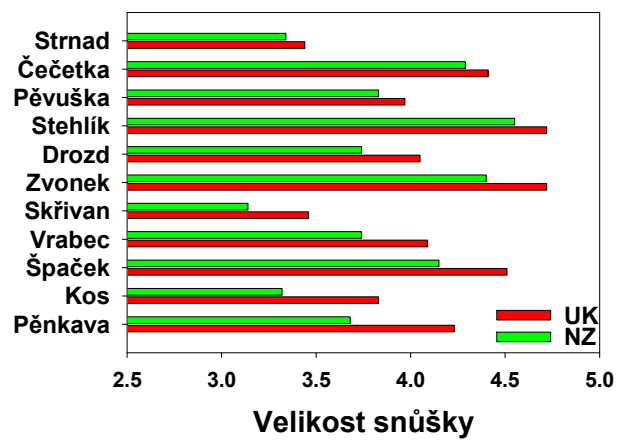


Hymenops perspicillatus

Latitudinální gradient velikosti snůšky



Latitudinální gradient velikosti snůšky: přirozený experiment



Evans et al. Funct. Ecol. 2005

Tradiční vysvětlovací obsese: potravní nabídka

Lack D. 1968: *Ecological Adaptations for Breeding in Birds*. Důraz na:

- 1) evoluci velikosti snůšky
- 2) úlohu dostupnosti potravy v její evoluci
- 3) ptáky mírného pásma

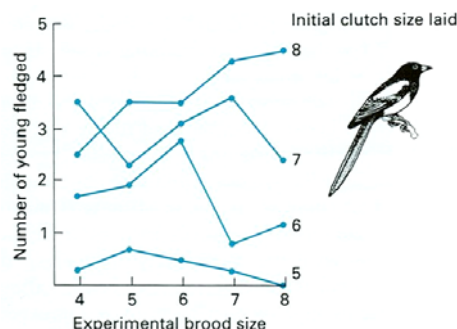
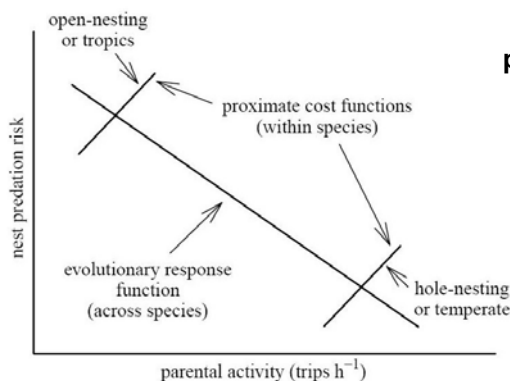


Fig. 1.7 Experiments on clutch size in magpies. Pairs which had initially laid 5, 6, 7 or 8 eggs were given experimentally reduced or enlarged broods. Pairs which had naturally laid large clutches did better with large broods and vice versa. From Högestedt (1980).



Fatální omyl: variabilita vnitrodruhová ≠ mezidruhová



proximální vs. ultimální vysvětlení

(Grim Vesmír 2000)

Figure 1. Skutch's (1949) hypothesis is based on opposite proximate and evolutionary relationships (Martin 1996a; Martin *et al.* 2000). Nest predation is expected to increase with parental activity within species yielding positive proximate cost functions within species or populations. Species or populations in environmental conditions with higher ambient levels of nest predation (e.g. open nests versus hole nests or lowland tropical versus temperate locations) should evolve lower activity (numbers of trips to the nest per hour), yielding a negative evolutionary function across species or populations.

Martin *et al.* Proc. R. Soc. 2000

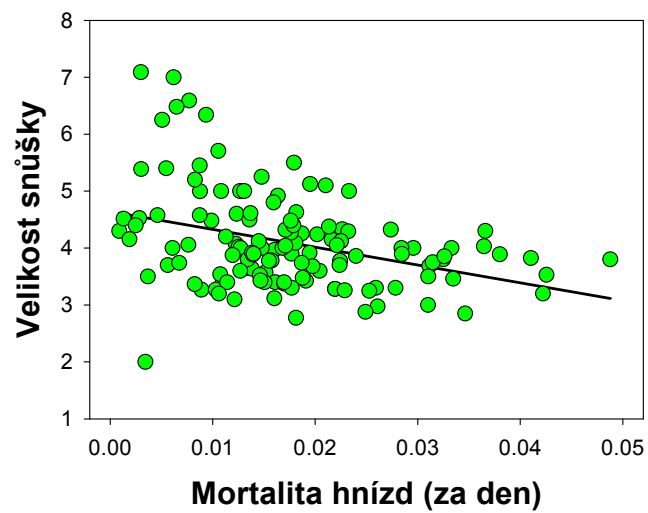
Nová vysvětlovací obsese: smrt

life-history theory = teorie životních stylů

- vysoká mortalita **mláďat** $\Rightarrow$ malá snůška
- vysoká mortalita **dospělců** $\Rightarrow$ velká snůška

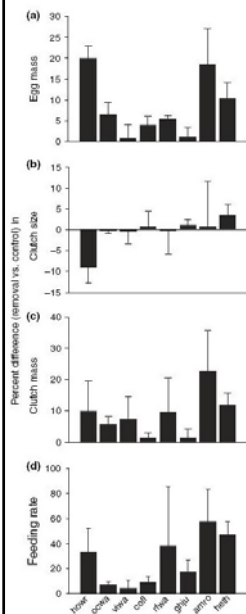


Žraní hnízd – predace



V. Remeš (vlastní data)

Aktuální riziko predace ovlivňuje rodičovské investice



Cardellina rubrifrons

Figure 2 Life history traits and parental care behaviours affecting offspring were altered by predator removals. Responses are illustrated by per cent change [(removal – control)/control × 100]. Females nesting on plots with reduced nest predation risk (a) laid larger eggs, (b) did not change their clutch size, but (c) increased clutch mass. Both parents (d) increased the rate they fed nestlings. Error bars indicate SEM across years.

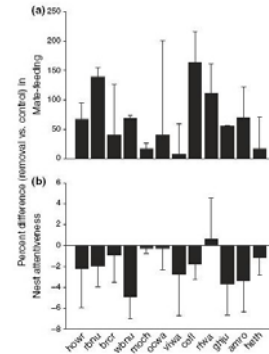


Figure 3 Behaviours affecting female parents were altered by predator removals. Responses are illustrated by per cent change [(removal – control)/control × 100]. Females nesting on plots with reduced nest predation risk (a) were fed more at the nest by their mates, and (b) reduced the percentage of time they spent incubating. Error bars indicate SEM across years.

Fontaine & Martin Ecol. Lett. 2006

Žraní hnízd – predace

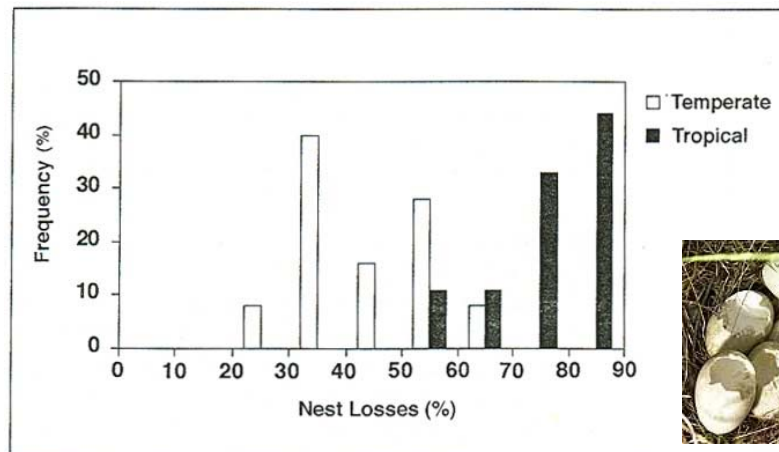


Figure 3.1

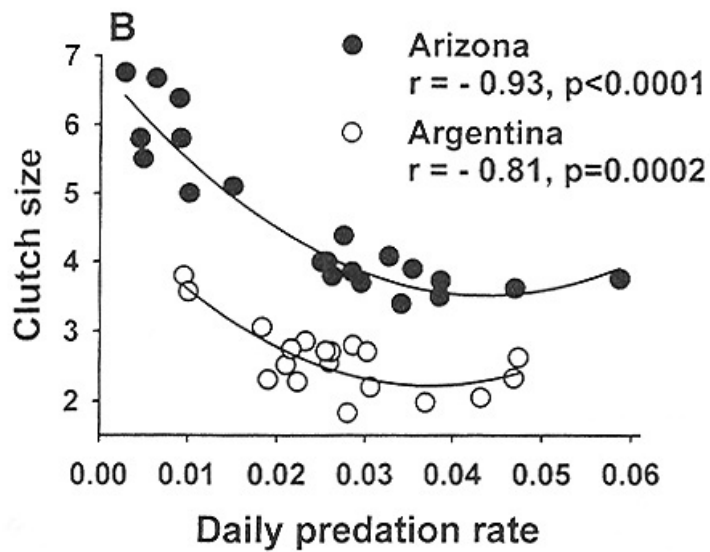
Frequency distribution of predation frequency on nests for studies on north temperate passerines (n = 25, Martin 1993) and Neotropical passerines (n = 9; Snow 1962, Morton 1971b and unpubl. data, Willis 1974, Oniki 1979, Wunderle 1982, Skutch 1985, Young 1994, Roper and Goldstein 1997, Woodworth 1997). Only studies with at least 100 nests monitored were included.

Žraní hnízd – predace



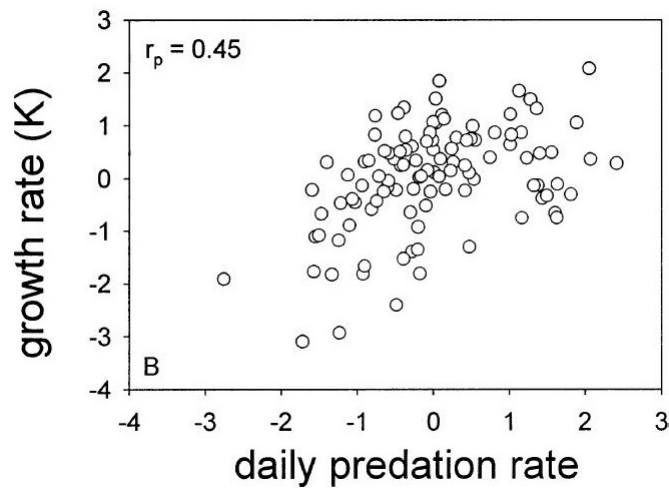
Nothura maculosa

Predace – hraje roli, ale nevysvětlí vše



Martin et al. Science 2000

Vliv rodičovské péče: korelace



Remeš & Martin Evolution 2002

Vliv rodičovské péče: korelace

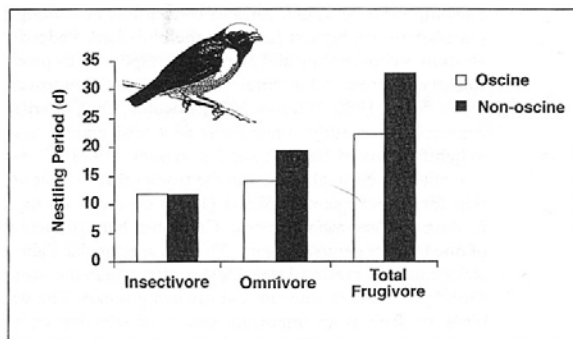


Figure 7.3

Average duration of nestling period for total insectivores, adult frugivores and total frugivores (like the Yellow-crowned Euphonia shown), for oscines and non-oscines. Data from Skutch (1954, 1960, 1969) and Snow (1970). Drawing from Skutch (1954).

Paradox inkubační periody

- tropy: *pomalý* růst mláďat
- *nízká* frekvence krmení
- plody – málo energie
- krátký den (12 hod.)

horší dostupnost potravy:

1) stabilní, ale *nížší* potravní nabídka

2) vyšší kompetice (slabá sezonalita prostředí → populační hustoty u nosné kapacity prostředí → málo zdrojů per capita)

**Žraní dospělců:
tropická dlouhověkost
vs.
„mírný“ mráz a tah**



Vliv rodičovské péče: korelace

- life-history theory:
- trade-off between current and future reproduction
- **residual reproductive value:**
riskovat smrt rodičů, nebo mláďat?



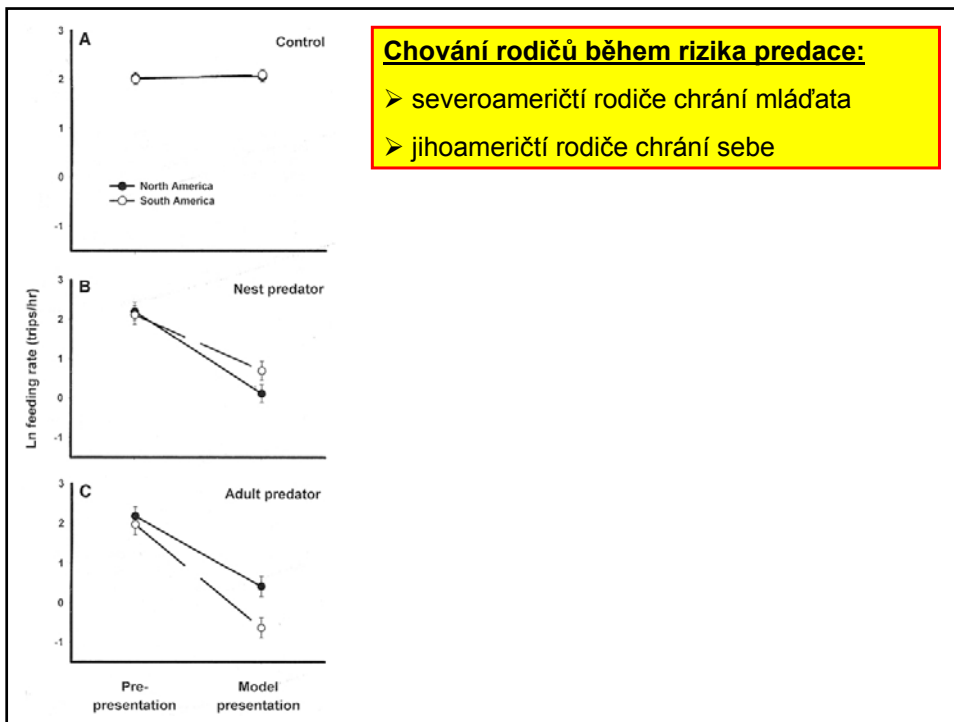
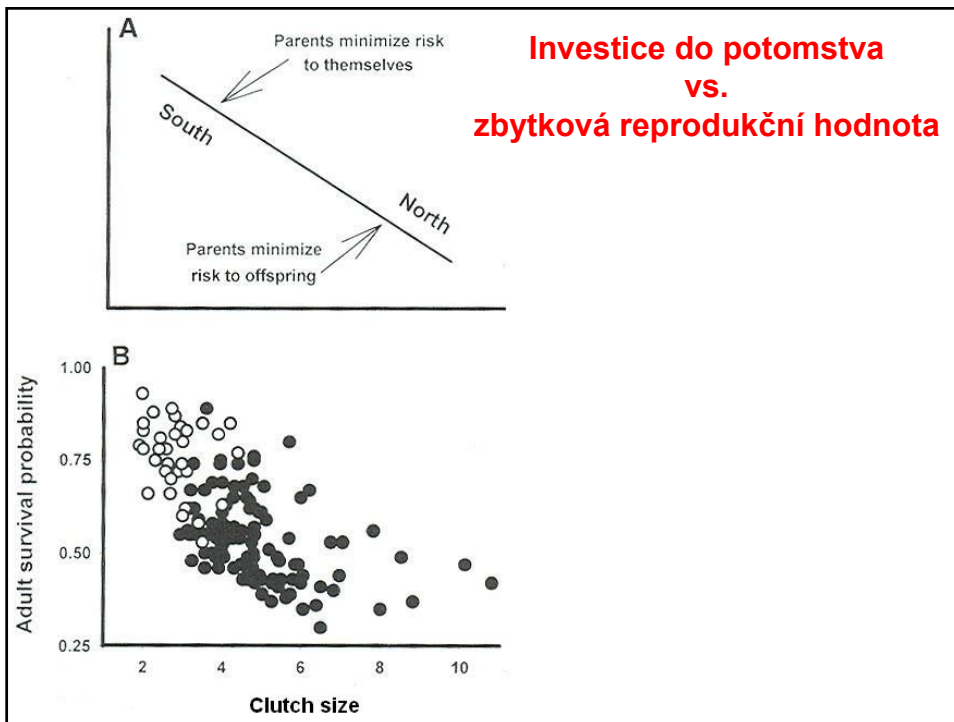
- Arizona vs. Argentina

reakce na:

- 1) sojka (predátor mláďat)
- 2) krahujec (predátor rodičů)
- 3) kontrola (tangara: nežere ani rodiče, ani mláďata)



Ghalambor & Martin Science 2001



Načasování hnízdění vs. potravní nabídka

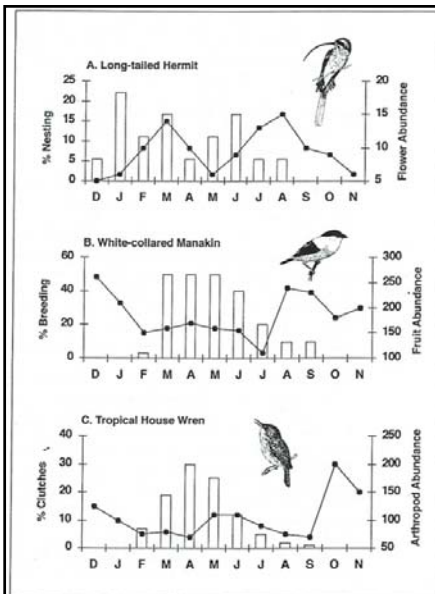
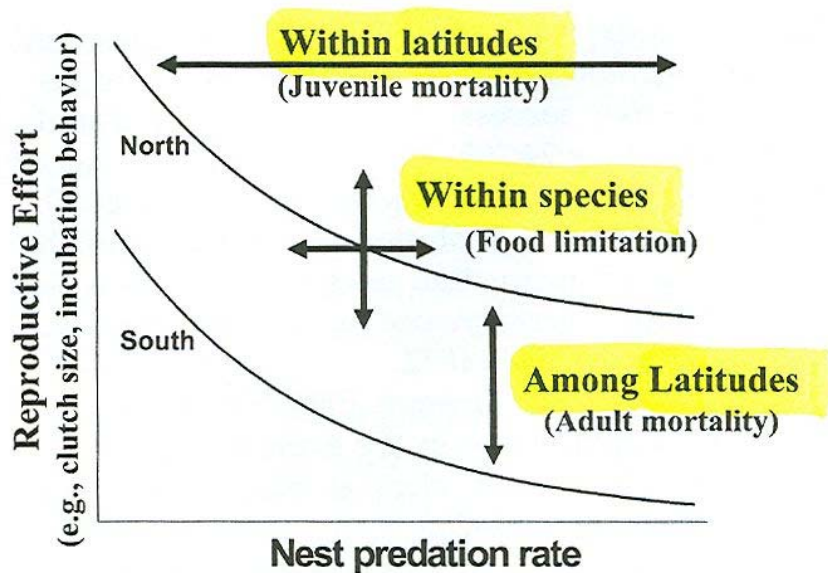


Figure 2.2
Timing of breeding and food abundance for A) Long-tailed Hermit, *Phaethornis superciliosus* (Stiles 1980; % nests started and number of foodplants in full bloom), B) White-collared Manakin, *Manacus candei* (Levey 1988; % individuals captured in breeding condition and total number plants with ripe fruit) and C) Tropical House Wren, *Tropodectes aedon* (Young 1994; % clutch initiations and arthropod biomass). Drawings from Blake (1953).



Shrnutí: hierarchický model reprodukčních investic



Martin Auk 2004

Velikost vejce

Velikost vejce: nejen velikost snůšky a rodiče

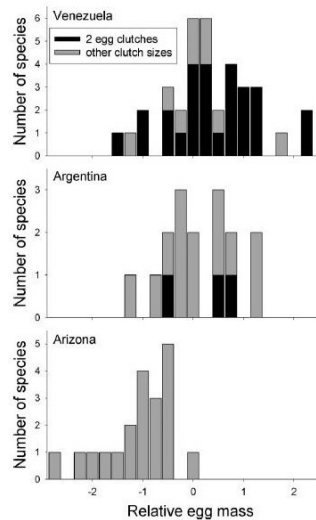


Fig. 1. Distribution of variation in relative egg mass (corrected for adult mass) among 72 passerine species studied at three sites: tropical Venezuela, subtropical Argentina, and north temperate Arizona. Relative egg masses for species with a clutch size of two eggs (i.e., mean clutch size >1.9 and <2.1 eggs) are indicated by black bars to illustrate that the full range of variation in relative egg mass exists for a constant clutch size.

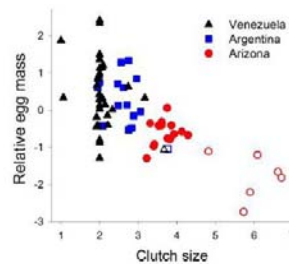


Fig. 2. Relative egg mass (corrected for adult mass) and clutch size of passerine species among three sites. Relative egg mass was greater in species with smaller clutch sizes based on study of 72 passerine species in tropical Venezuela, subtropical Argentina, and north temperate Arizona, but relative egg size varies substantially for a given clutch size in tropical Venezuela and subtropical Argentina. Open symbols are cavity-nesting species.

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Velikost vejce: nejen velikost snůšky a rodiče

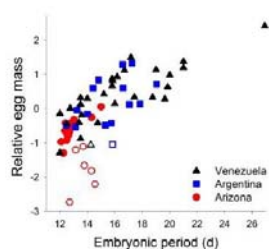


Fig. 4. Relative egg mass (corrected for adult mass) is greater in species with longer embryonic periods (d) among 64 passerine species in tropical Venezuela, subtropical Argentina, and north temperate Arizona. Open symbols reflect cavity-nesting species and show an interacting effect where their larger clutches are associated with relatively smaller eggs (Fig. 2).

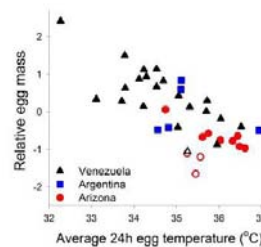


Fig. 3. Relative egg mass (corrected for adult mass) and average egg temperature over 24-h periods. Relative egg mass is greater in species where parental inattentiveness causes lower egg temperatures based on study of 37 passerine species in tropical Venezuela, subtropical Argentina, and north temperate Arizona. Open symbols are cavity-nesting species and show an interacting effect where their larger clutches are associated with relatively smaller eggs (Fig. 2).

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Inkubační perioda

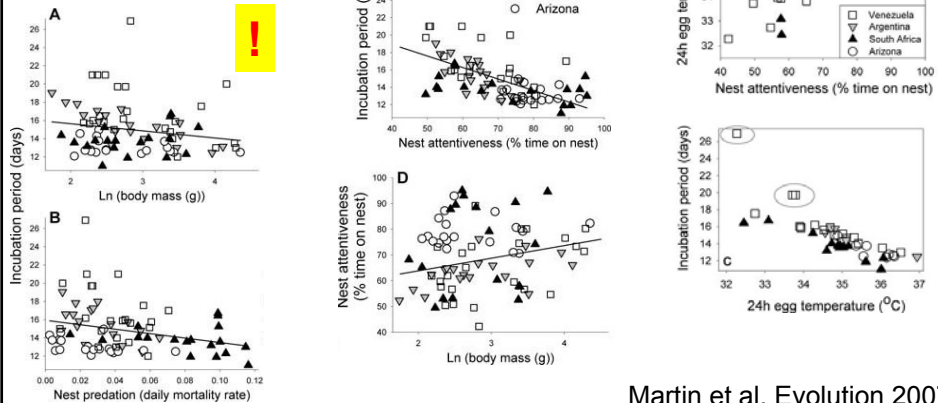
Inkubační perioda: predace a alometrie

Teorie:

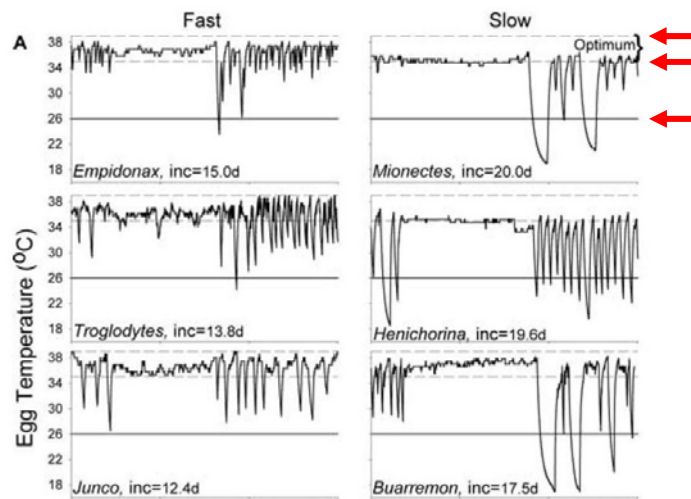
velikost rodiče $\rightarrow$ délka embryonálního vývoje

predace $\rightarrow$ délka embryonálního vývoje

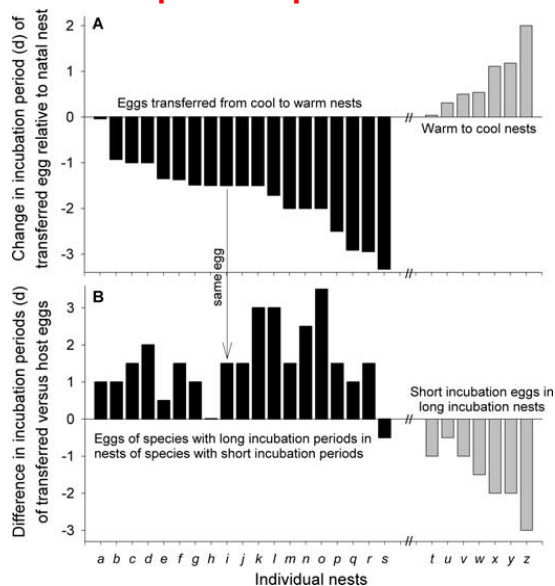
Empirie:



Inkubační perioda: predace a alometrie



Inkubační perioda: predace a alometrie



Martin et al. Evolution 2007

Shrnuto a sečteno:

	mírný pás	tropy
mortalita dospělců	~ 50%	~ 20%
mortalita hnízd	~ 50%	~ 75%
velikost snůšky	4 – 6	2
velikost vejce	malá	velká
kladení	denně	často obden
počet snůšek/rok	1 – 2	4 – 5
věk první reprodukce	nižší	vyšší
hnízdní období	3 – 4 měsíce	6 – 10 měsíců
čas hnízdění určuje	potravní nabídka	predace, pelichání, sex
variabilita hnízdění	minimální	obrovská
inkubace	♀	♂ + ♀
krmení mláďat	♀ > ♂	♂ + ♀
frekvence krmení	vysoká	nízká
délka rodičovské péče	krátká	dlouhá

Shrnuto a sečteno:

	mírný pás	tropy
hmyzožravost	zcela dominantní	méně běžná
plodožravost	velmi vzácná	velmi běžná
totální plodožravost	totálně chybí	vzácná
„food limitation“	–	+
„cost of reproduction“	+	–
obrana teritoria	hnízdni období	celoročně
filopatrie	slabá	maximální
teritoria	malá	~ 10x větší
determinanty repr. úspěchu	inkubace, krmení	obrana hnízda, znovuzahnízdění
výběr	partnera	teritoria

Shrnuto a sečteno:

	mírný pás	tropy
pohlavní role	divergence	konvergence
pohlavní	dimorfismus	monomorfismus
zpěv	♂	♂ + ♀
zpívají	hodně	velice málo
zpěvní aktivita	v hnízdni období	celoročně
hlavní funkce zpěvu	přilákání partnerů	obrana teritoria
EPC	běžné	vzácné
monogamie	sociální	genetická
hladina testosteronu	proměnlivá, vysoká	trvale nízká

Společný jmenovatel: tropičtí ptáci žijí pomalu

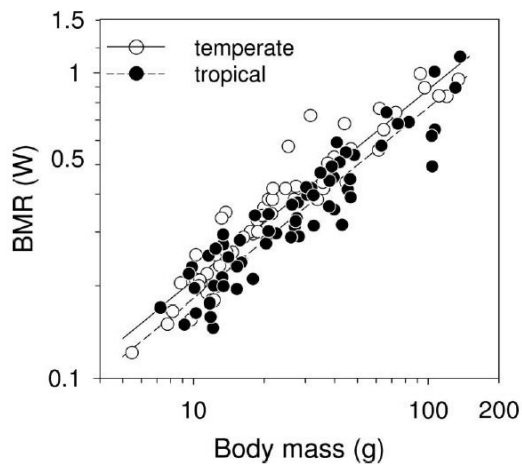


Fig. 1. BMR (W) as a function of body mass (g) in tropical and temperate birds. Open circles, temperate species; filled circles, tropical species; solid and dashed line, result of a general linear model for, respectively, temperate and tropical species.

Wiersma et al. PNAS 2007

Ale pozor na generalizace: tropy nejsou homogenní prostředí!!!

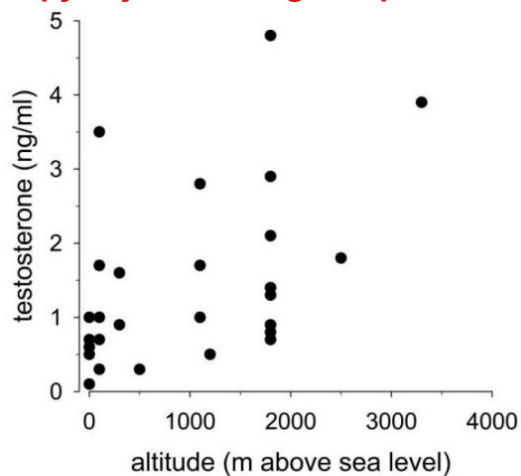


Figure 4: Elevation of the study site above sea level and testosterone concentrations.

Goymann et al. Am. Nat. 2004



Suma sumárum:
„Tropical birds break all the rules“

ptáci mírného pásma ➔ rychlé strategie
ptáci tropického pásma ➔ pomalé strategie

ptáci mírného pásma ☹ abiotická selekce
ptáci tropického pásma ☺ biotická selekce

„Because of their worldwide dominance, tropical birds typify the adaptive realm of birds and it is their natural history that should be viewed as the norm for birds.“

(Stutchbury & Morton 2001)