



NOAA HIHWNMS



W. Hodge



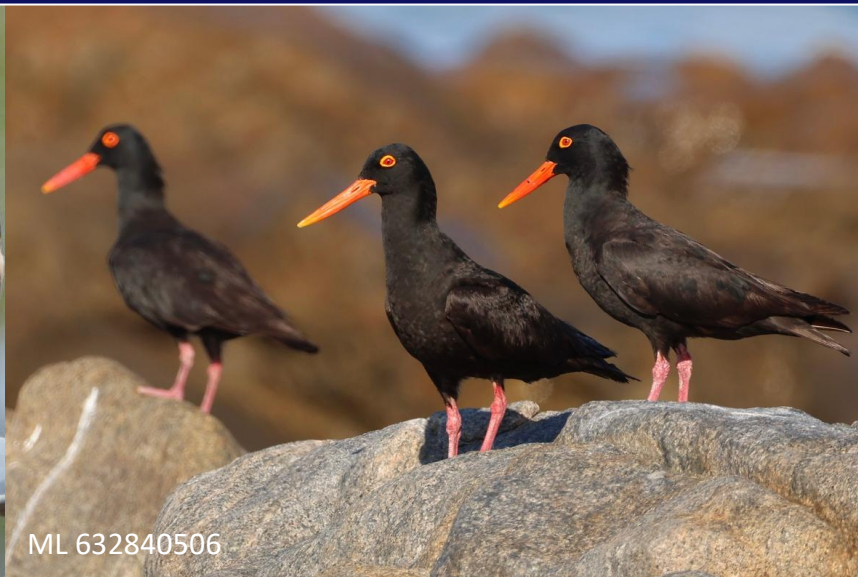
NOAA Fisheries

Migration and Philopatry in Long-lived Vertebrates

Eleanor Gnam
22 May 2025



ML 70617551



ML 632840506



Monterey Bay Aquarium

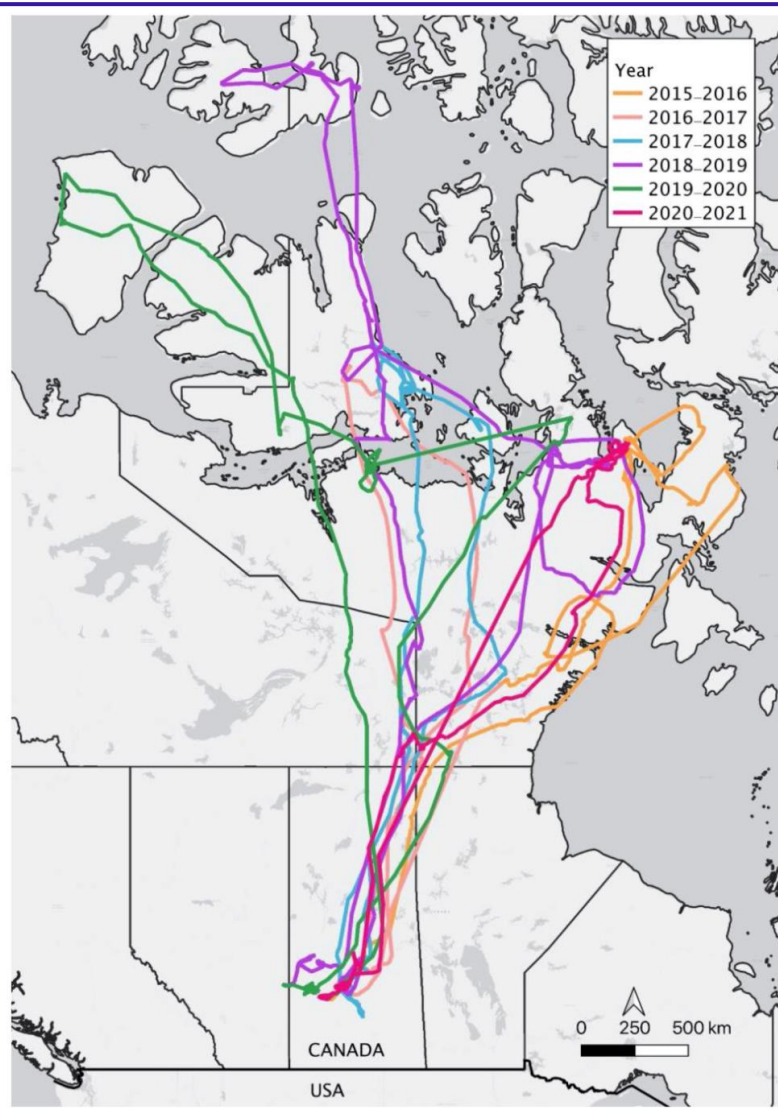
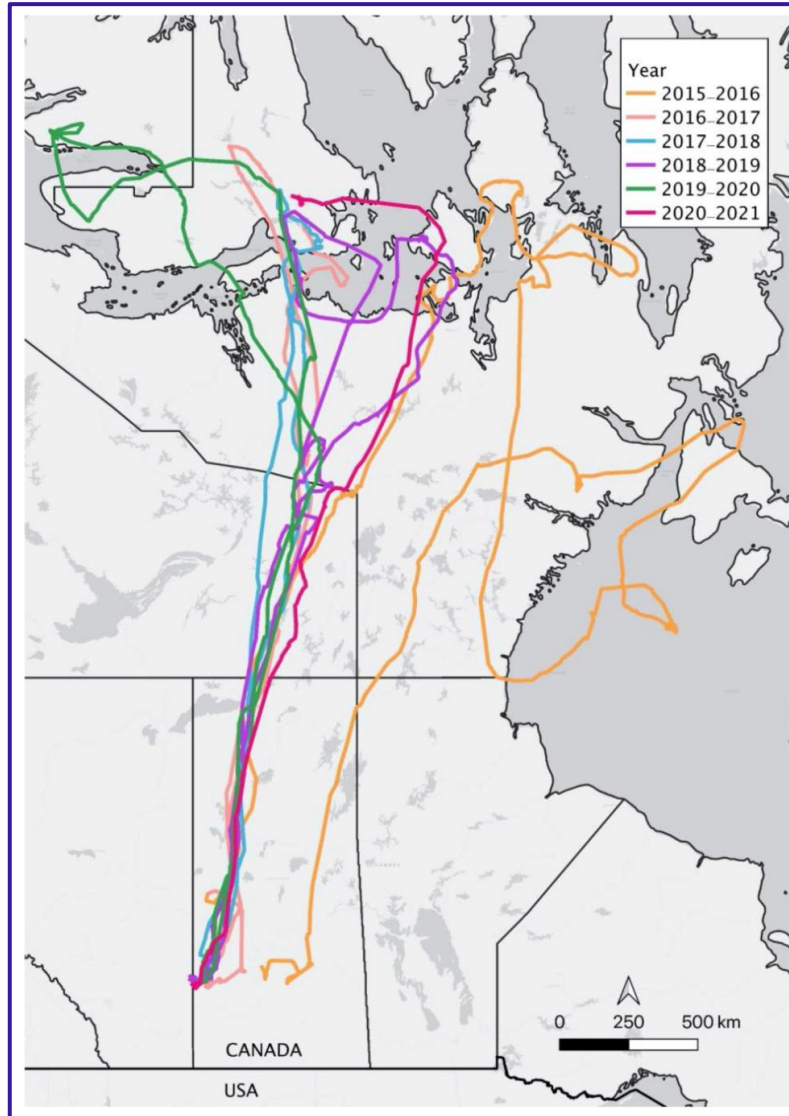
Outline

Presentation Outline

- Introduction
- Definitions
- Dispersal
- Seasonal Migration
- Discussion

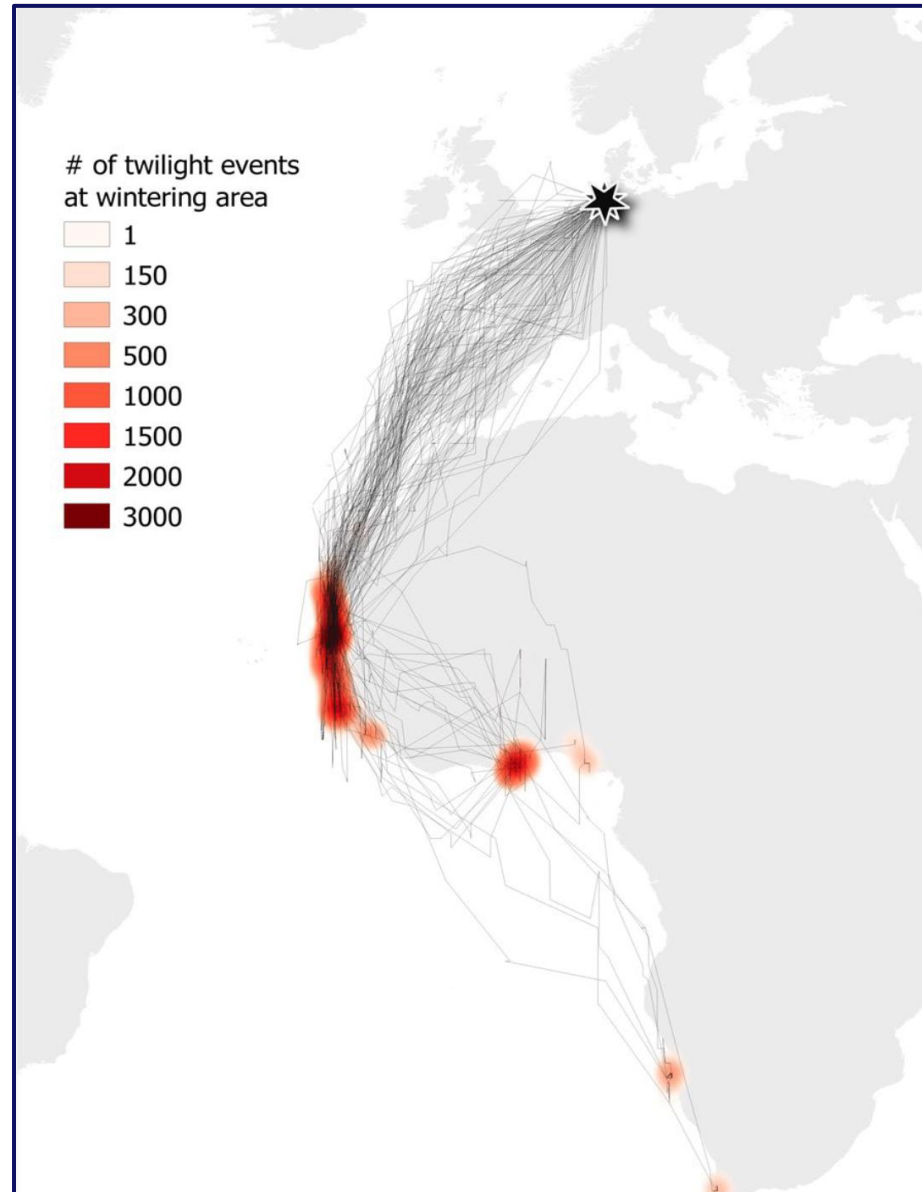
- **“Migration confers flexibility on life histories and allows choices of where and when to breed.”** – Dingle, H. (1985). Migration and Life Histories. *Migration: Mechanisms and Adaptive Significance*, 27, 27–42.
- **“Any discussion of dispersal is beset with problems of terminology.”** – Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, 28(4), 1140–1162.

Introduction



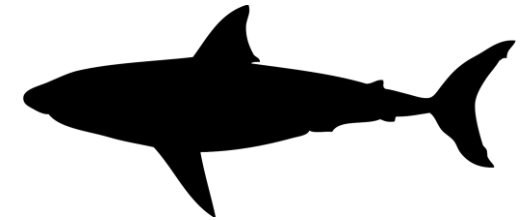
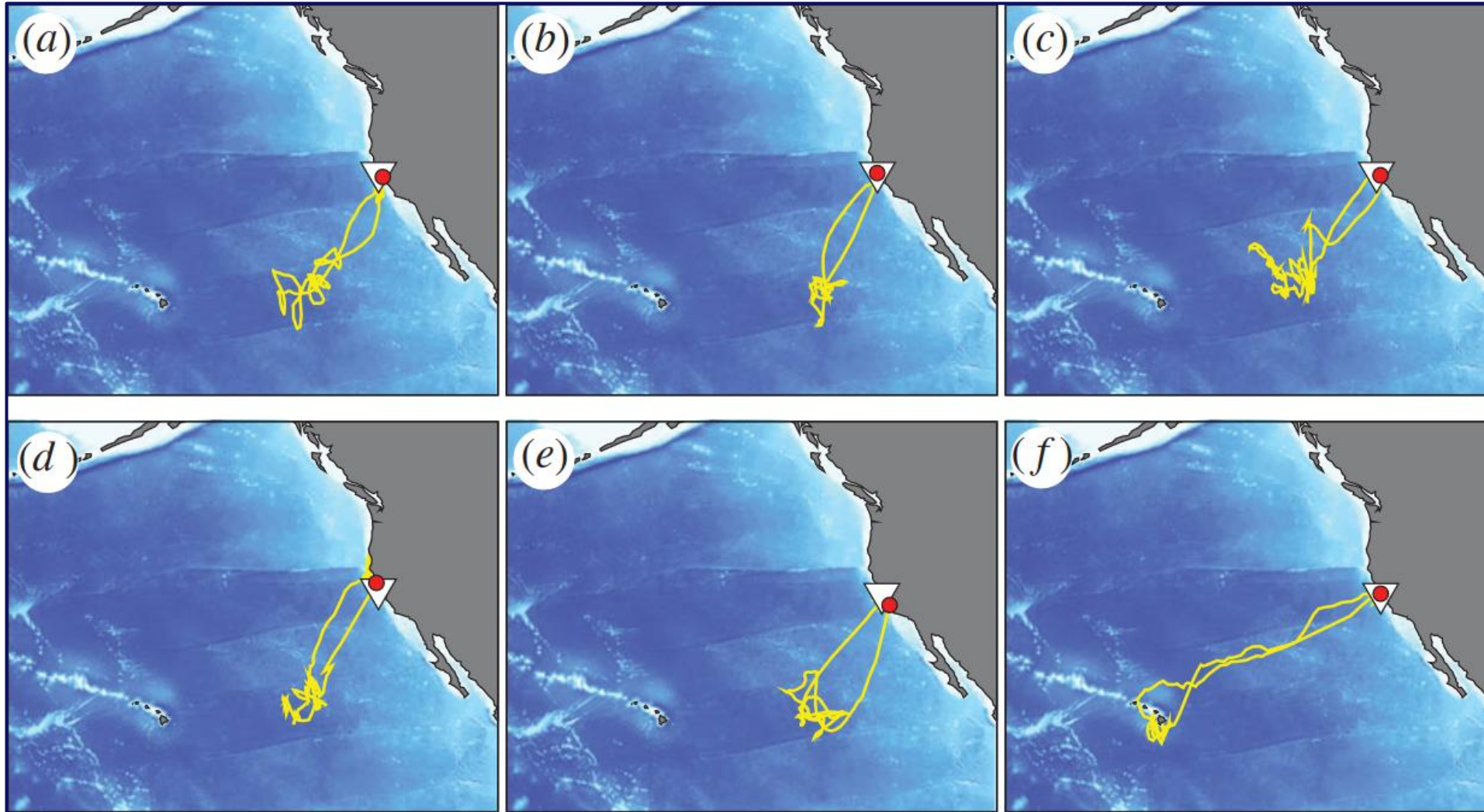
Wiebe, K. et al. (2023). Snowy Owls in central North America have regular migration and high philopatry to wintering sites though not always to home ranges. *Avian Conservation and Ecology*, 18(2)

Introduction



Kürten, N., et al. (2022). High individual repeatability of the migratory behaviour of a long-distance migratory seabird. *Movement Ecology*, 10(1), 5.

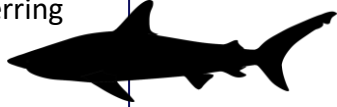
Introduction



Jorgensen, S. J., et al. (2010).
Philopatry and migration of Pacific
white sharks. *Proceedings of the Royal
Society B: Biological Sciences*,
277(1682), 679–688.

Philopatry: Conflicting Definitions

"...we apply the term philopatry...referring solely to the preferential return of reproducing individuals to their natal sites...resulting in the multigenerational use of these sites by distinct populations with their own internal dynamics." – Chapman, D. D., et al. (2015). There and Back Again: A Review of Residency and Return Migrations in Sharks, with Implications for Population Structure and Management. *Annual Review of Marine Science*, 7(1), 547–570.



"Ortstreue is the tendency of an animal to return to its birthplace or breeding place, particularly for breeding. The word 'philopatry' will be used as its English equivalent in this review." – Huntington, C. E. (1951). "Ortstreue" and Subspecies Formation in the Pied Flycatcher. *Ecology*, 32(2), 352–355.

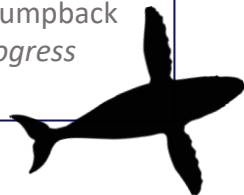


"philopatry (an urge to stay at its native locality)" – Mayr, E. (1963). *Animal Species and Evolution*. Harvard University Press.

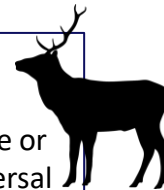
"Philopatry by our definition is attachment to a site, rather than to a conspecific individual or group of conspecifics." – Waser, P. M., & Jones, W. T. (1983). Natal Philopatry Among Solitary Mammals. *The Quarterly Review of Biology*, 58(3), 355–390.



"philopatry or natal philopatry — the faithful return of an individual to the site of its birth" – Baker, C., et al. (2013). Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Marine Ecology Progress Series*, 494, 291–306.



"We treat females as philopatric if they remain and breed in their natal range or group and we use natal dispersal to refer to permanent movement out of this area" – Clutton-Brock, T. H., & Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, 21(3), 472–492.



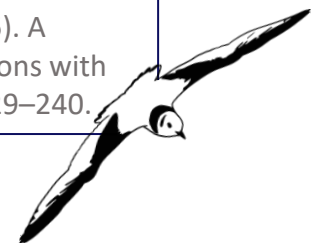
"Philopatry is defined as individuals frequently returning to or staying in their home ranges, birthplaces, or other specific localities." – Flowers, K., et al. (2016). A review of batoid philopatry, with implications for future research and population management. *Marine Ecology Progress Series*, 562, 251–261.



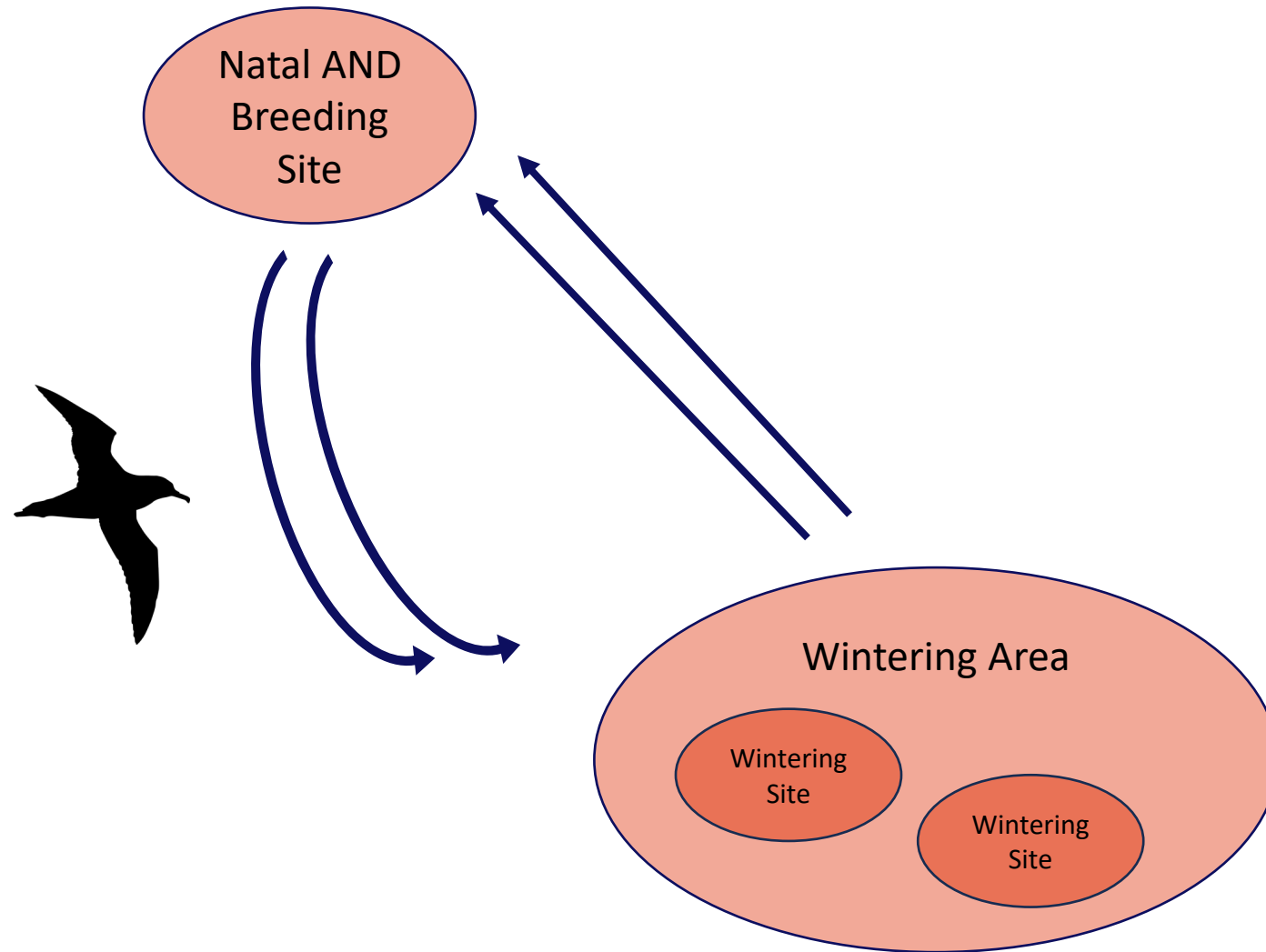
"Philopatry: Multiple-generation return of a population to a breeding site that leads to reproductive isolation" – Secor, D. H. (2015). *Migration Ecology of Marine Fishes*. Johns Hopkins University Press.



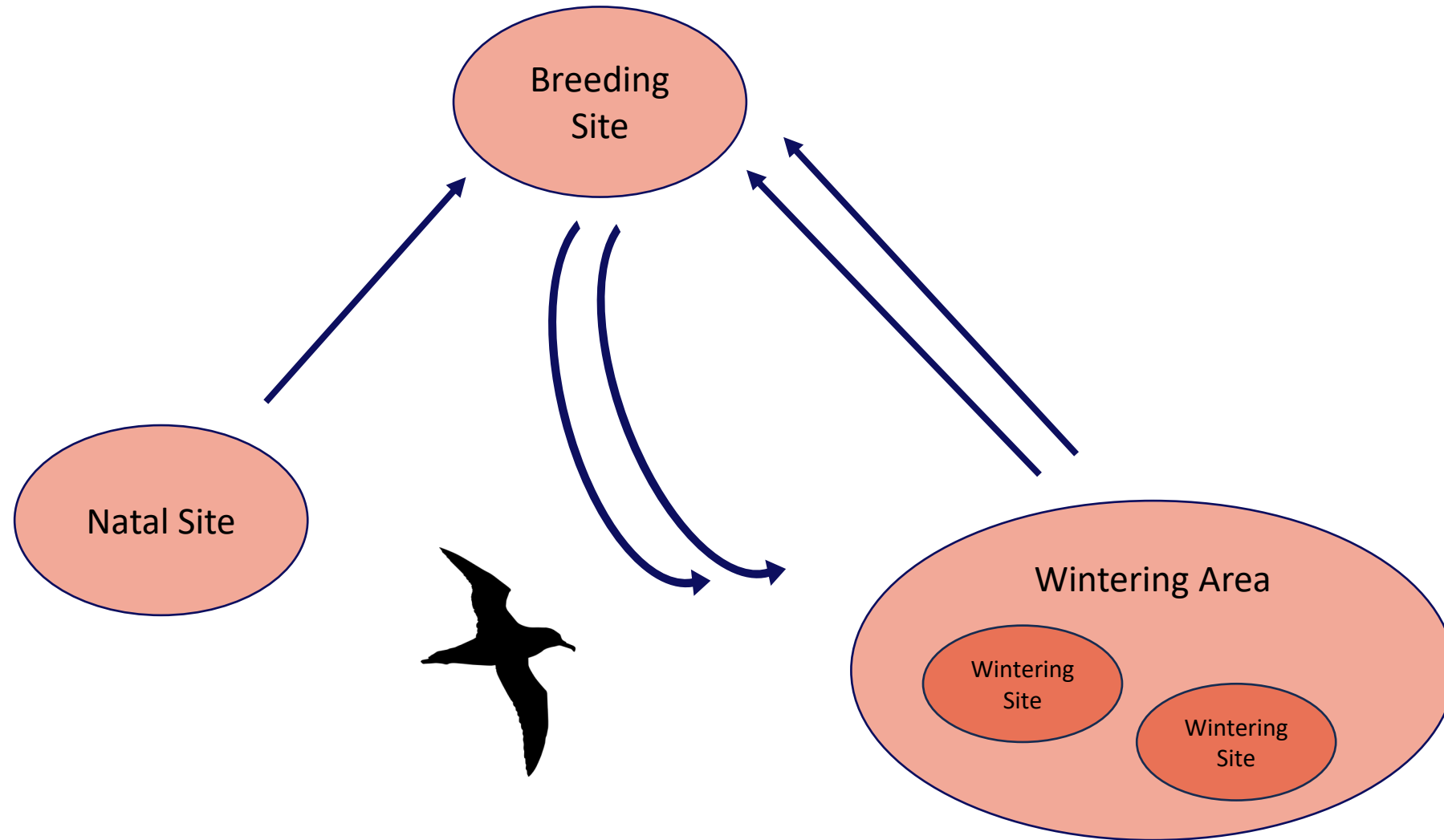
"...philopatry is used in its original and strict sense to describe the return of animals to breed in the area where they were reared" – Coulson, J. C. (2016). A Review of Philopatry in Seabirds and Comparisons with Other Waterbird Species. *Waterbirds*, 39(3), 229–240.



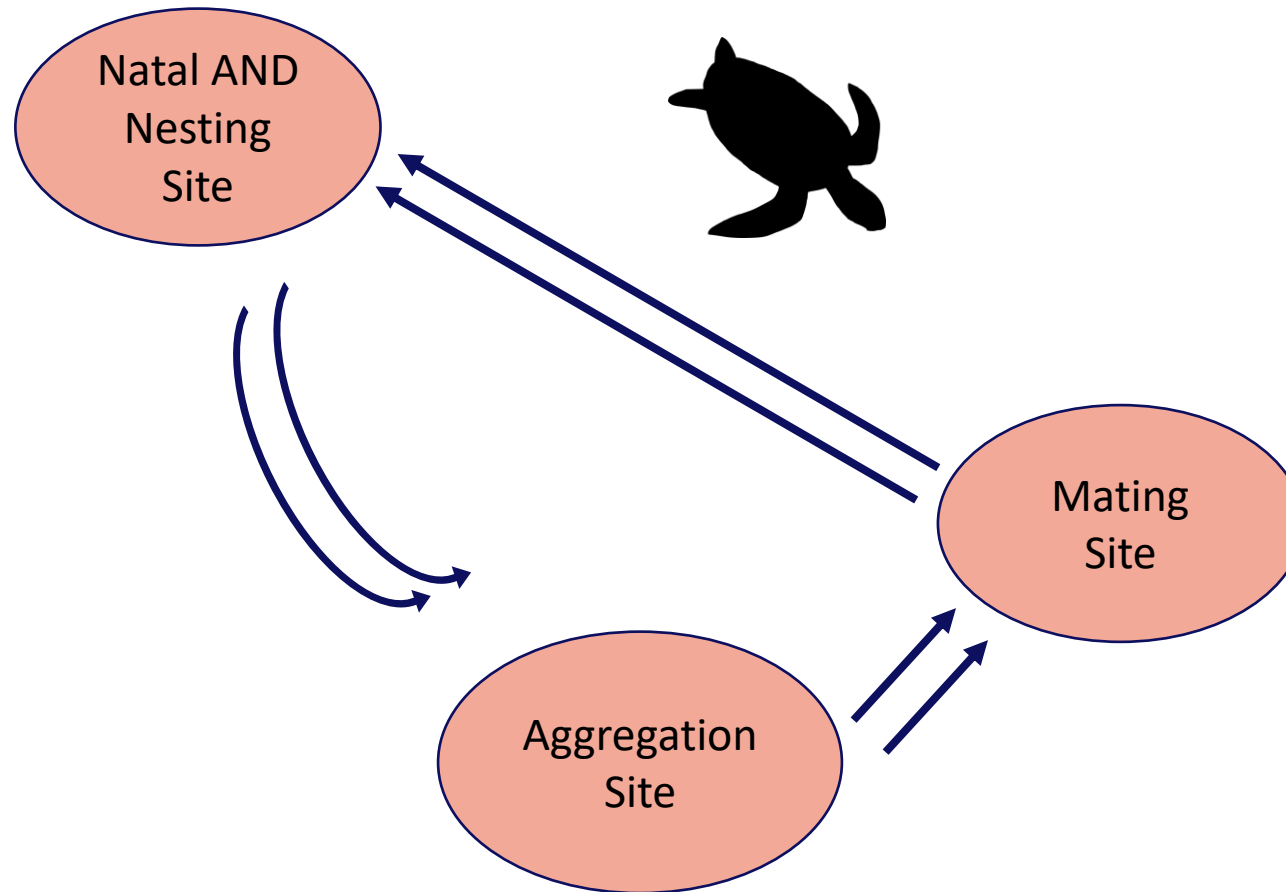
Philopatry: Types of Site Fidelity



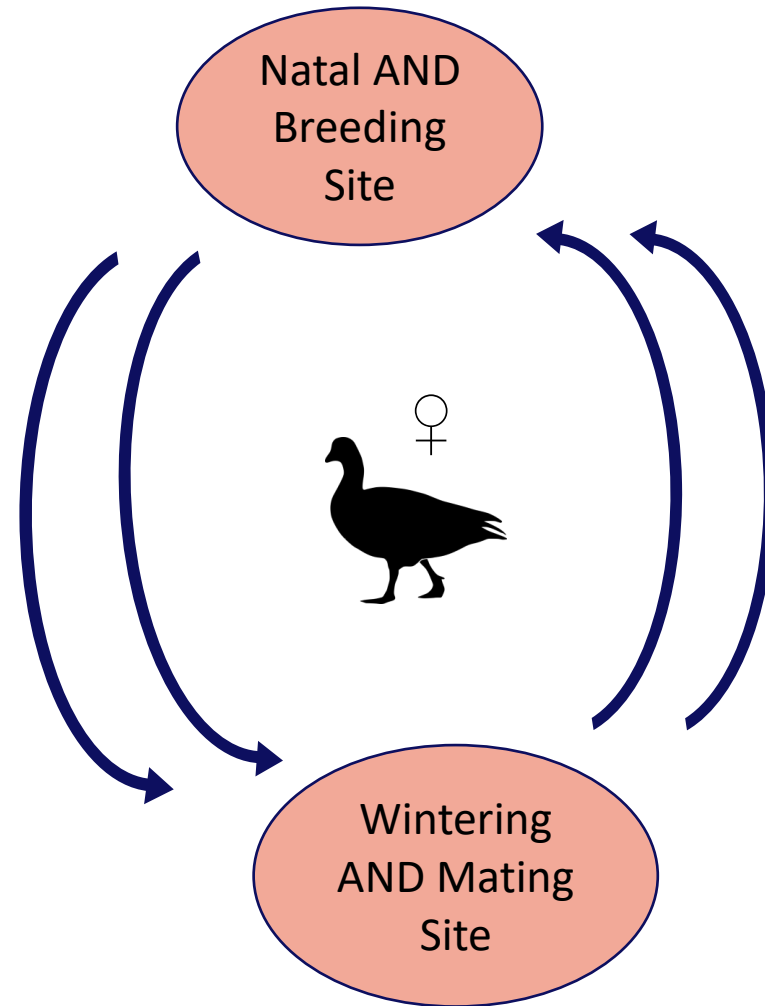
Philopatry: Types of Site Fidelity



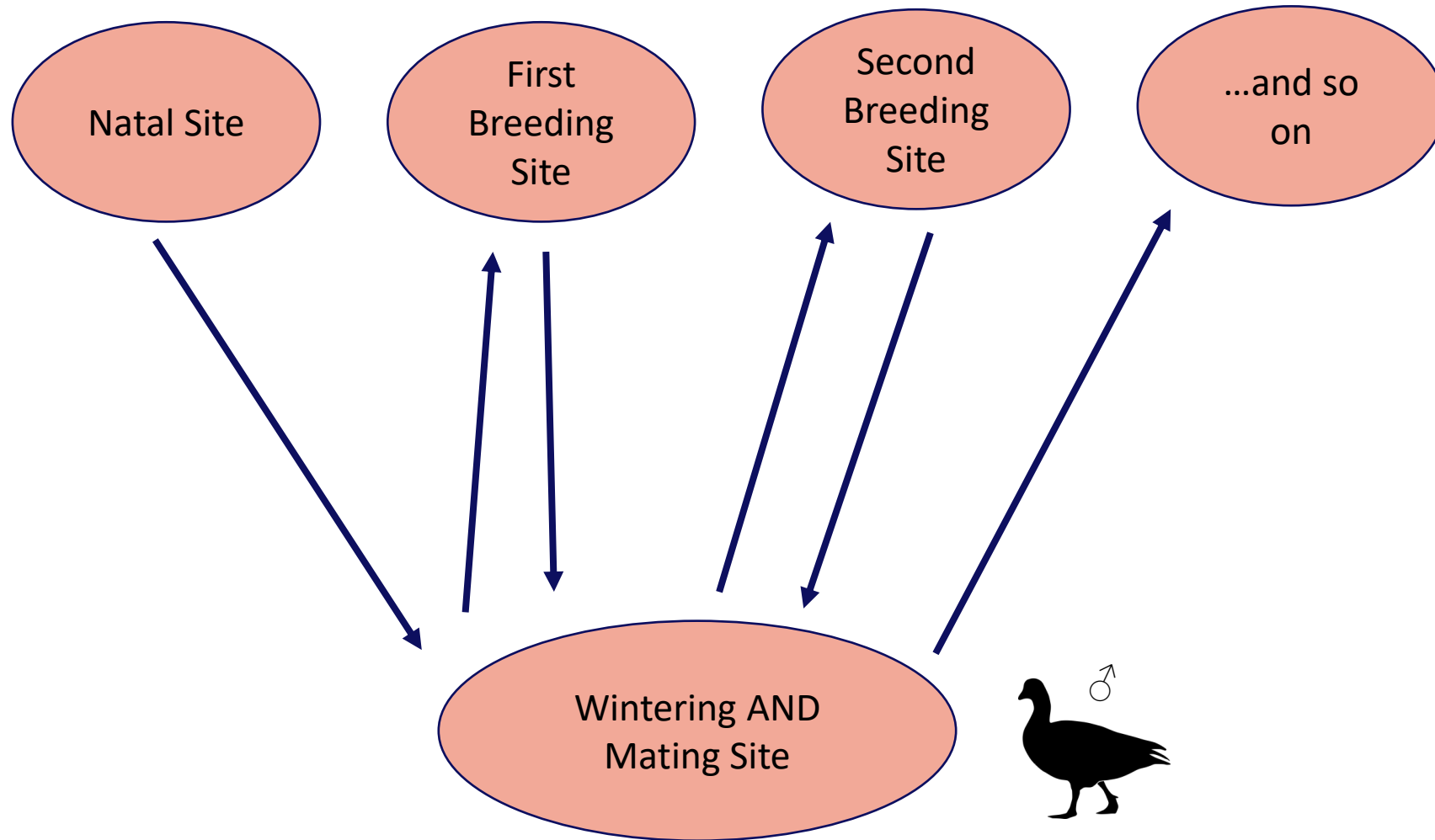
Philopatry: Types of Site Fidelity



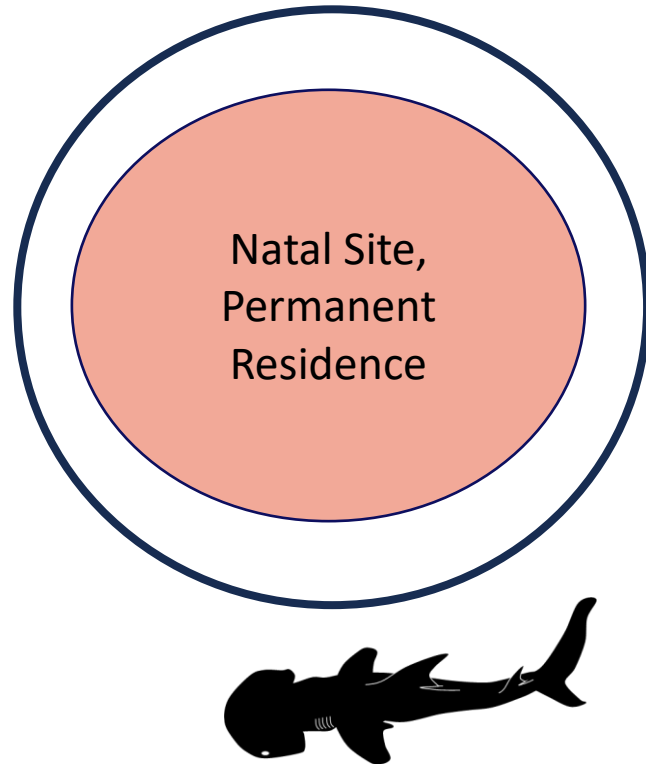
Philopatry: Types of Site Fidelity



Philopatry: Types of Site Fidelity

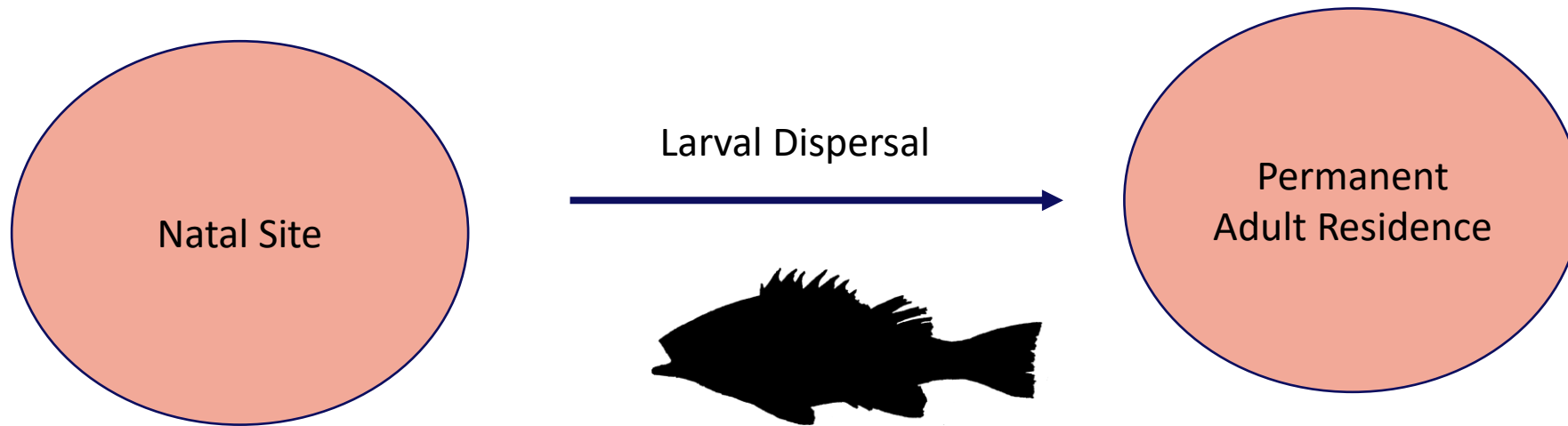


Philopatry: Types of Site Fidelity

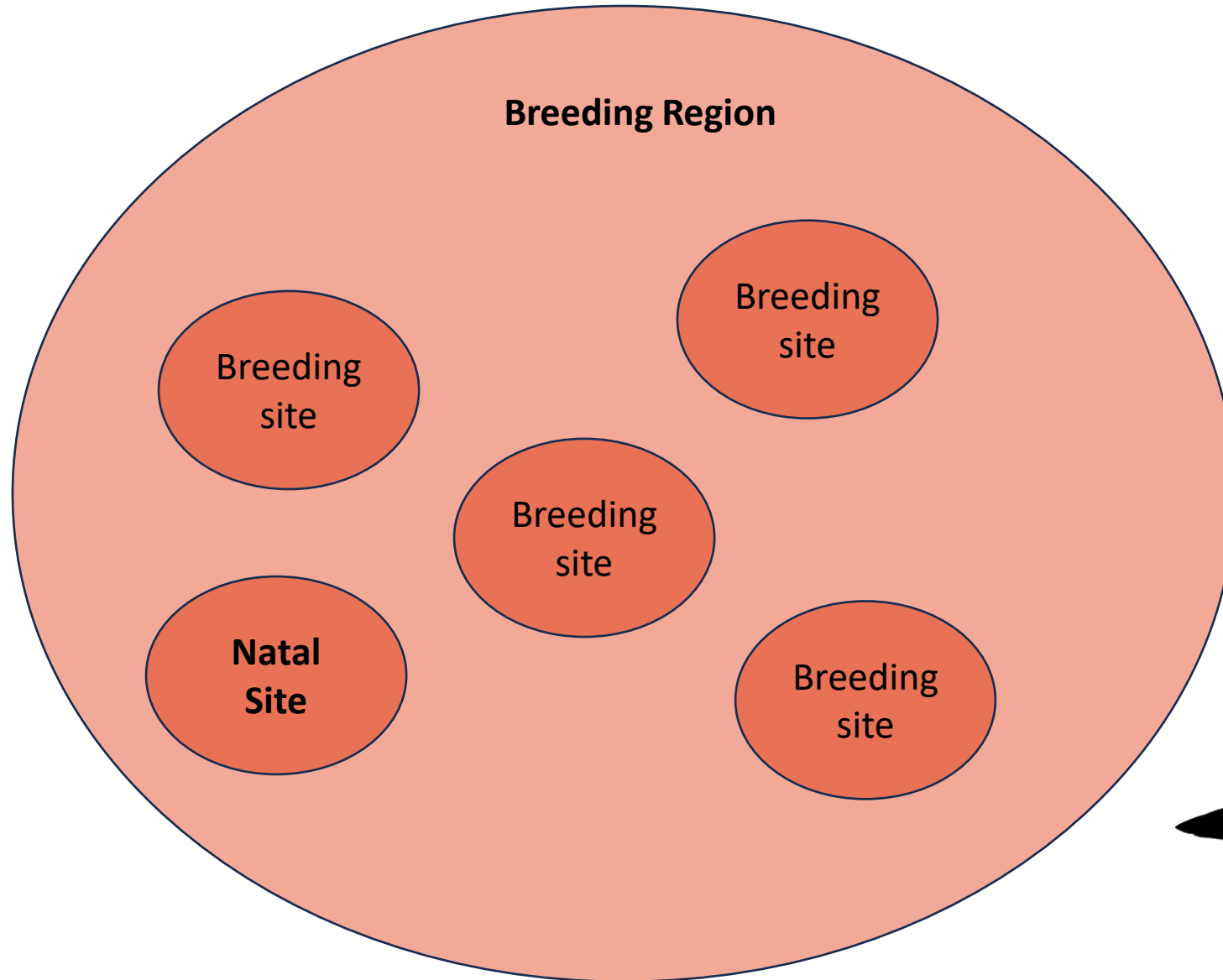


“Additionally, individuals that remain at their natal sites or regions and reproduce there simply because they do not leave are most accurately referred to as being **residential** or having limited dispersal **rather than being philopatric...**” – Chapman, D. D., et al. (2015). There and Back Again: A Review of Residency and Return Migrations in Sharks, with Implications for Population Structure and Management. *Annual Review of Marine Science*, 7(1), 547–570.

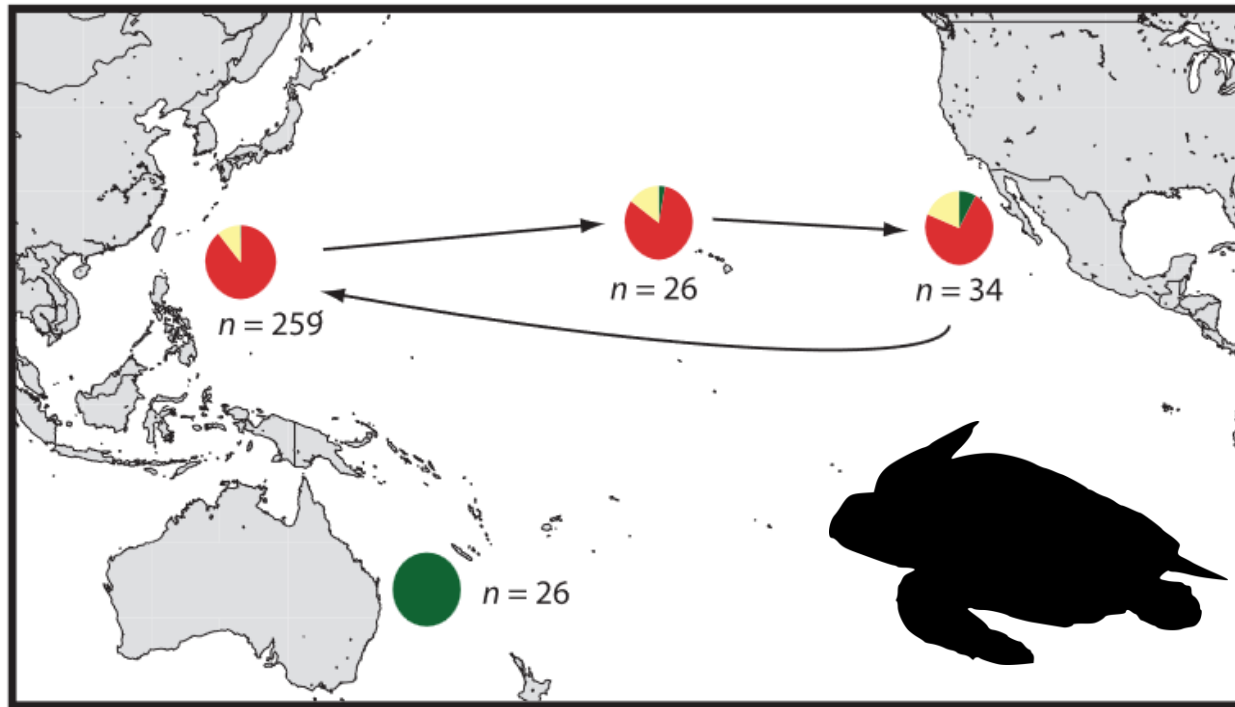
Philopatry: Types of Site Fidelity



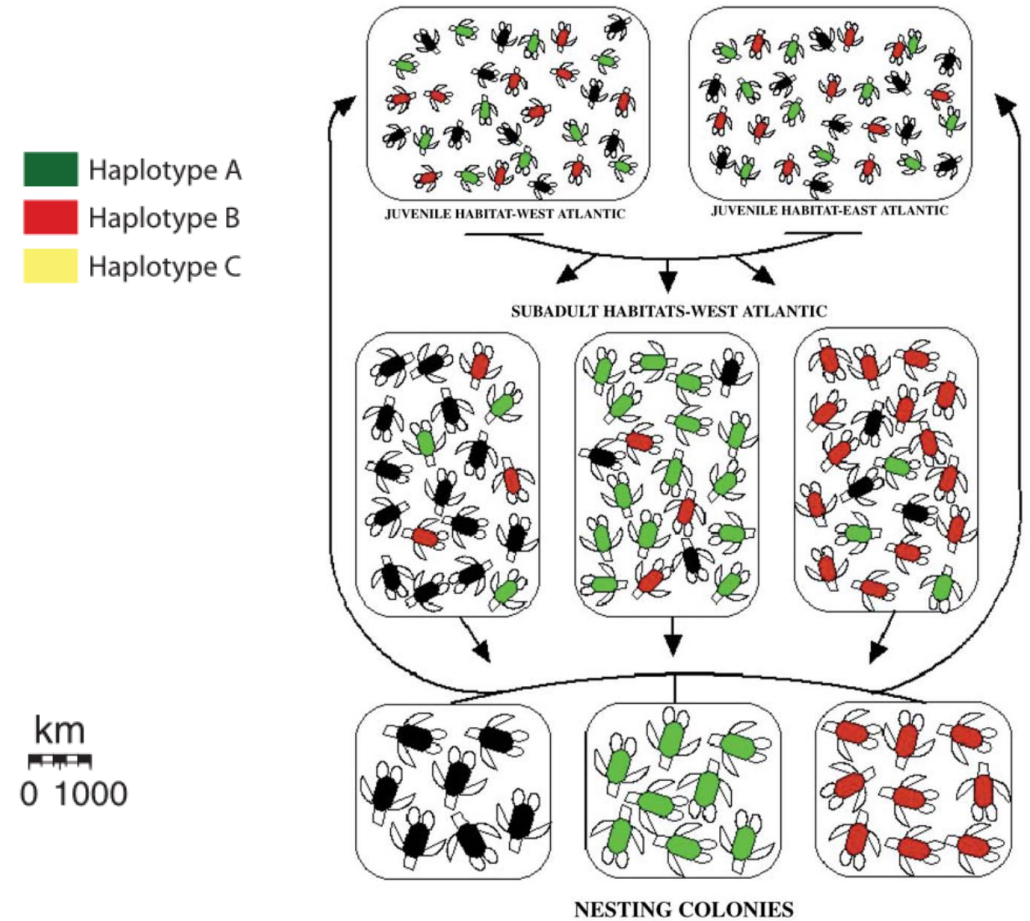
Philopatry: Scale



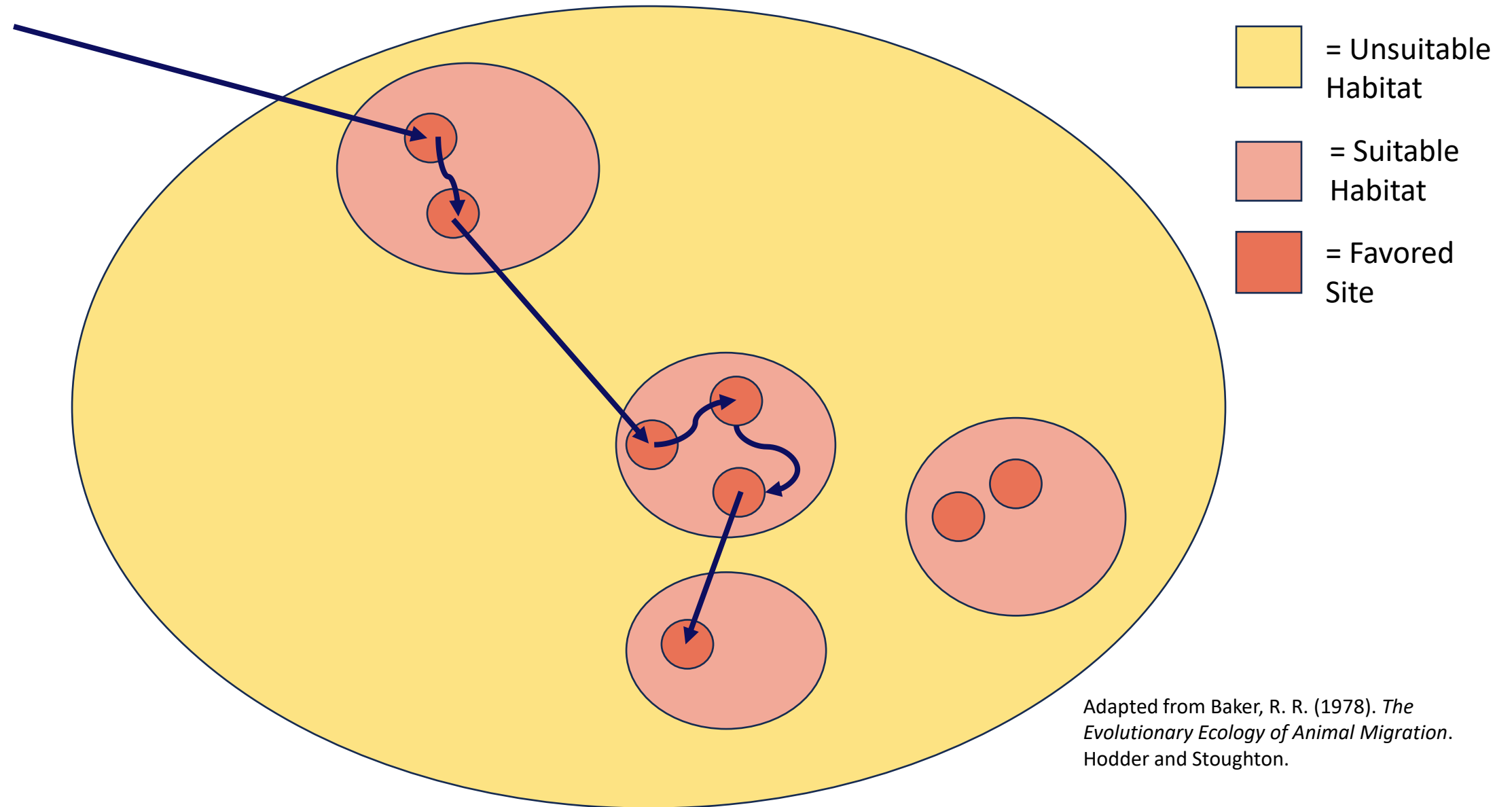
Philopatry: Population Structure



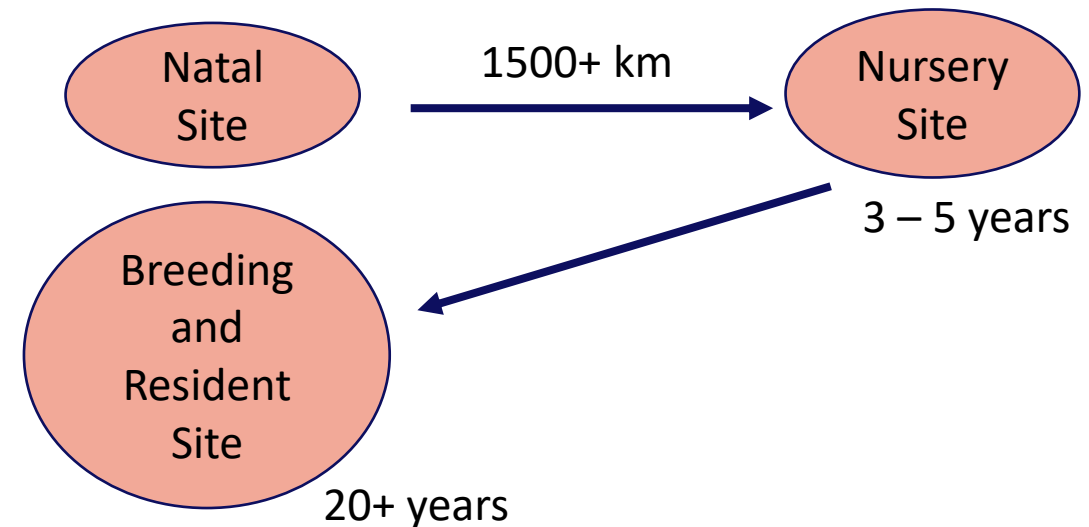
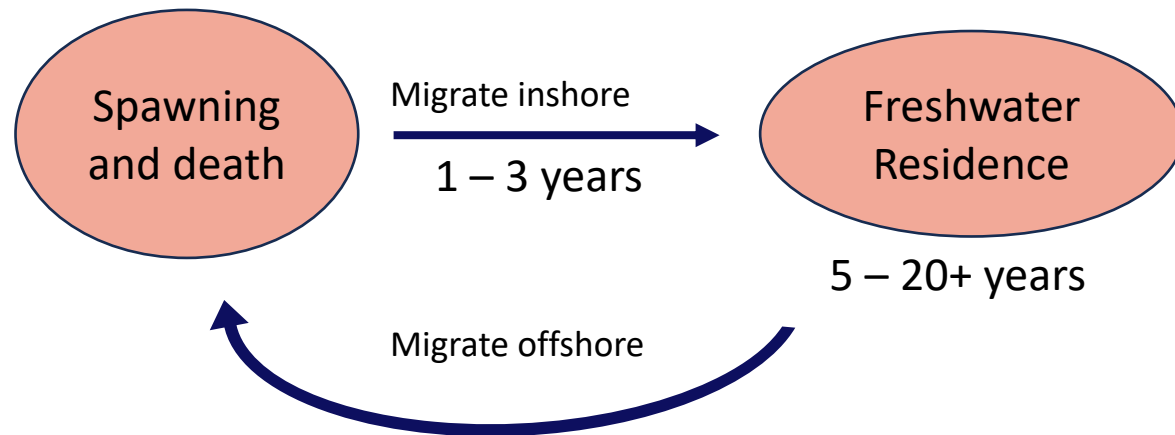
Bowen, B. W., & Karl, S. A. (2007). Population genetics and phylogeography of sea turtles. *Molecular Ecology*, 16(23), 4886–4907.



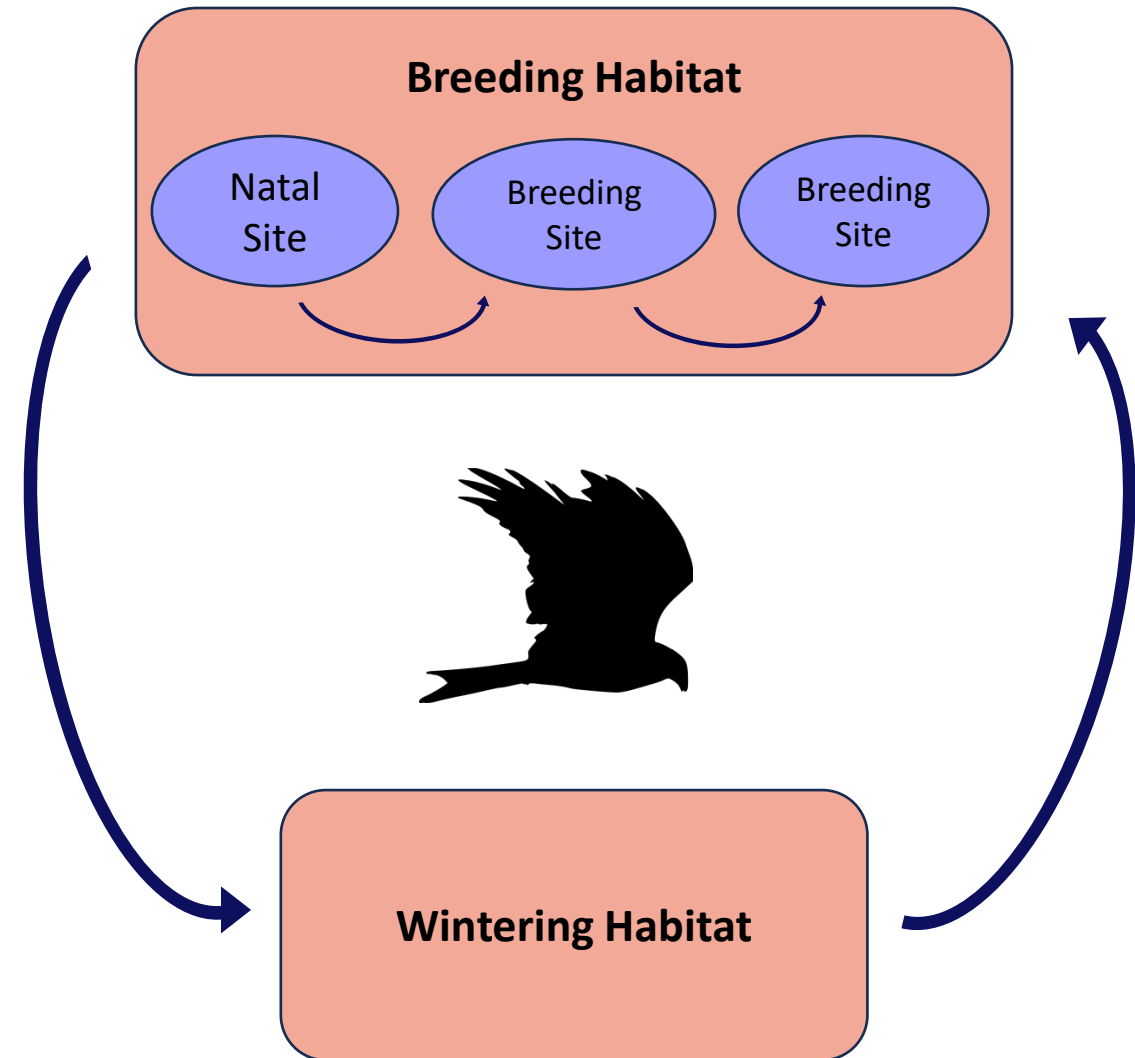
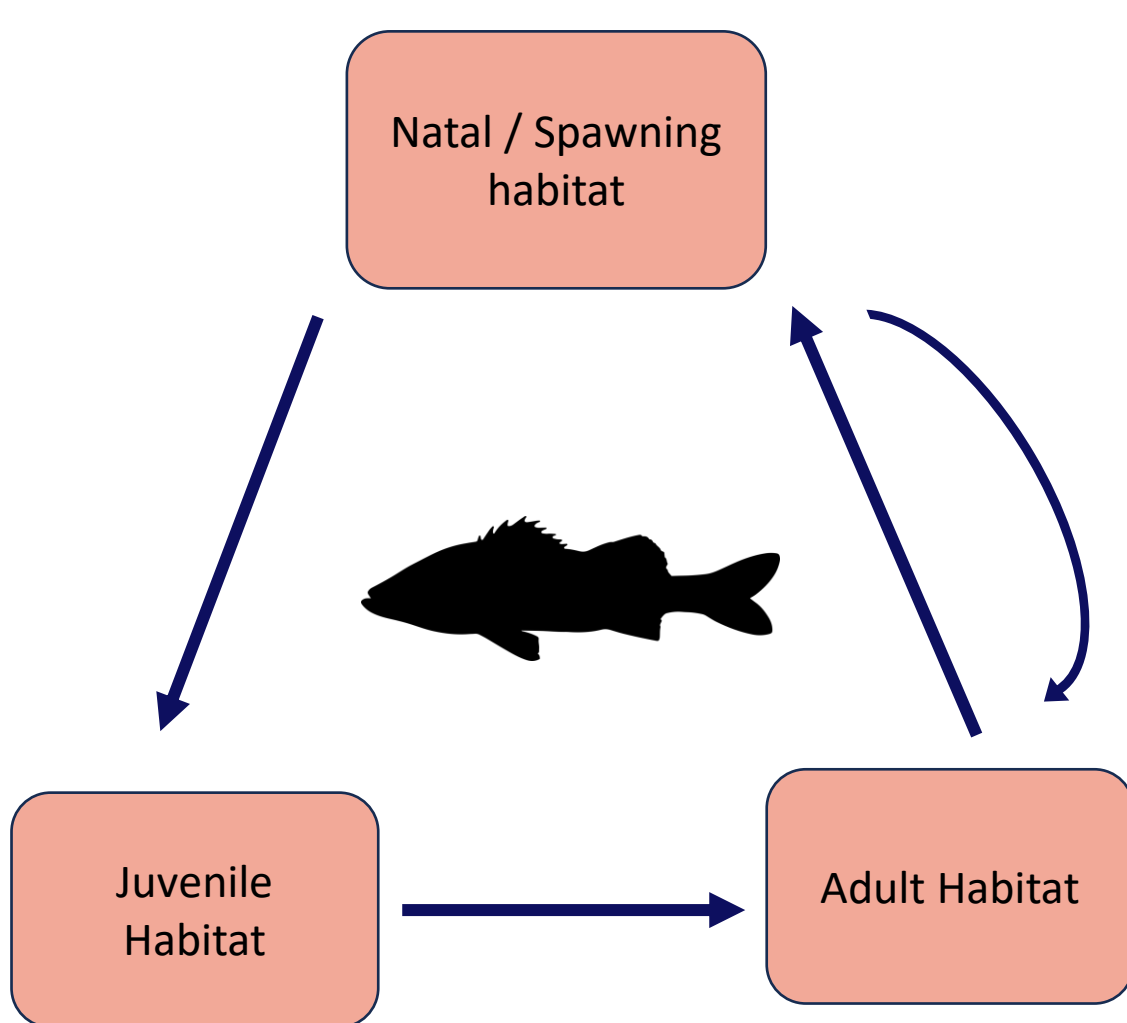
Migration: Scale



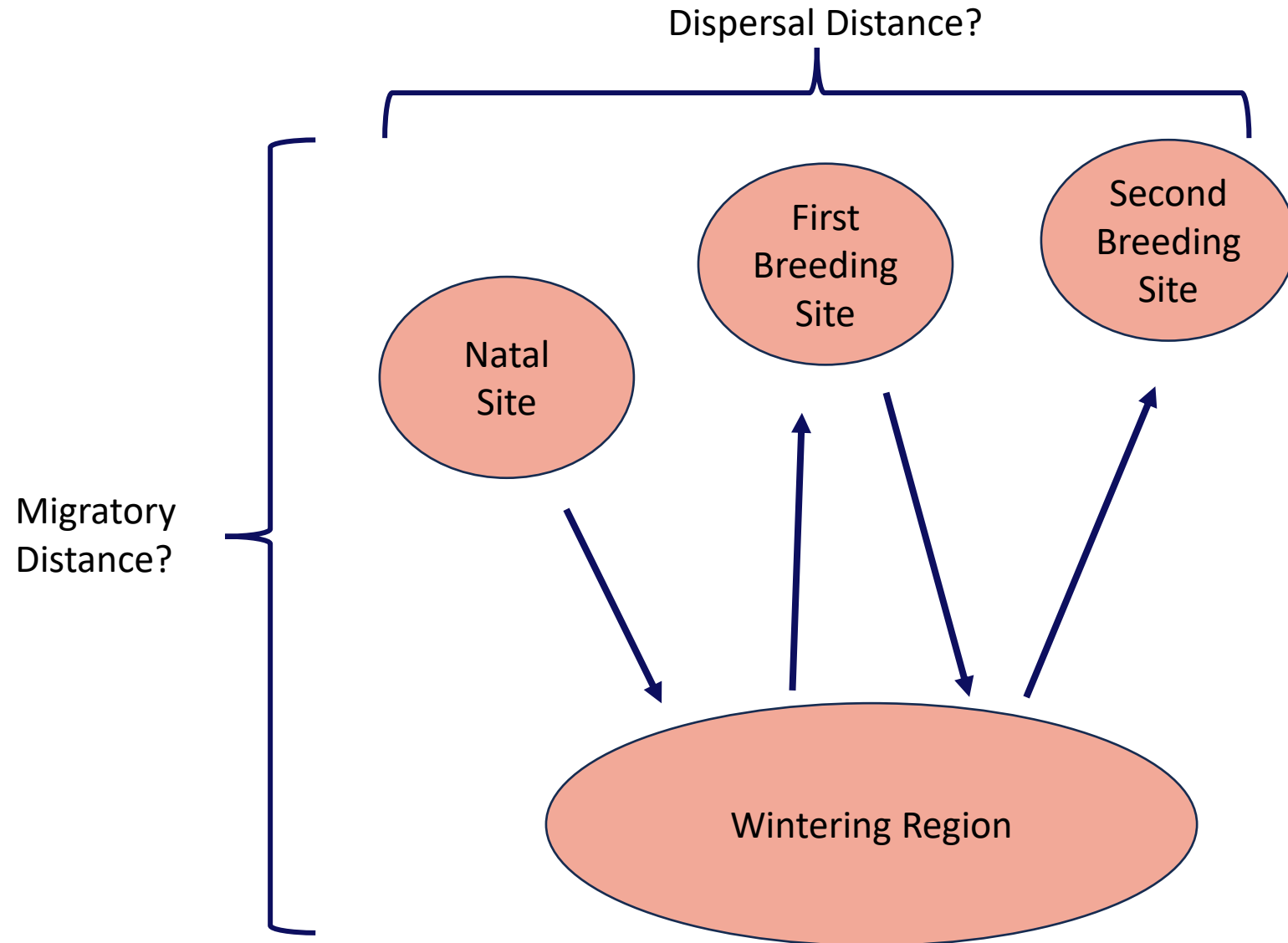
Migration: Repetition



Migration: Dispersal or No?

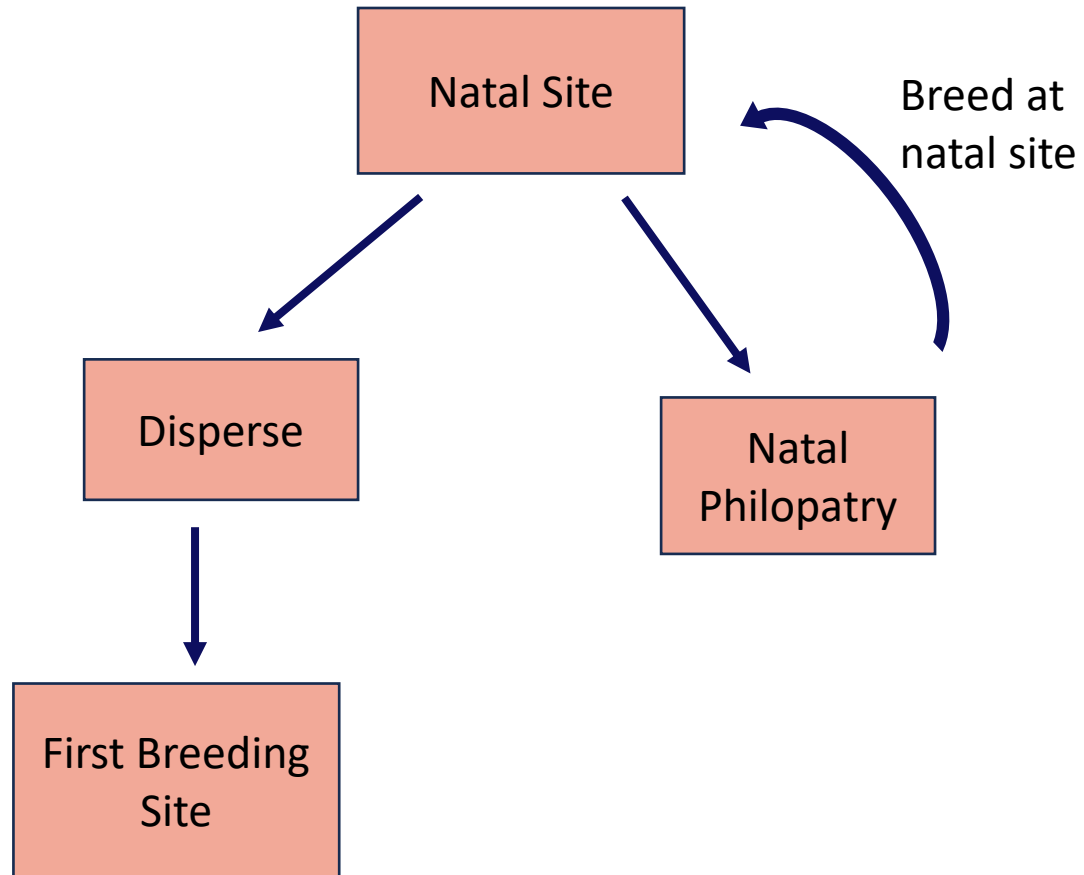


Migration: Dispersal or No?

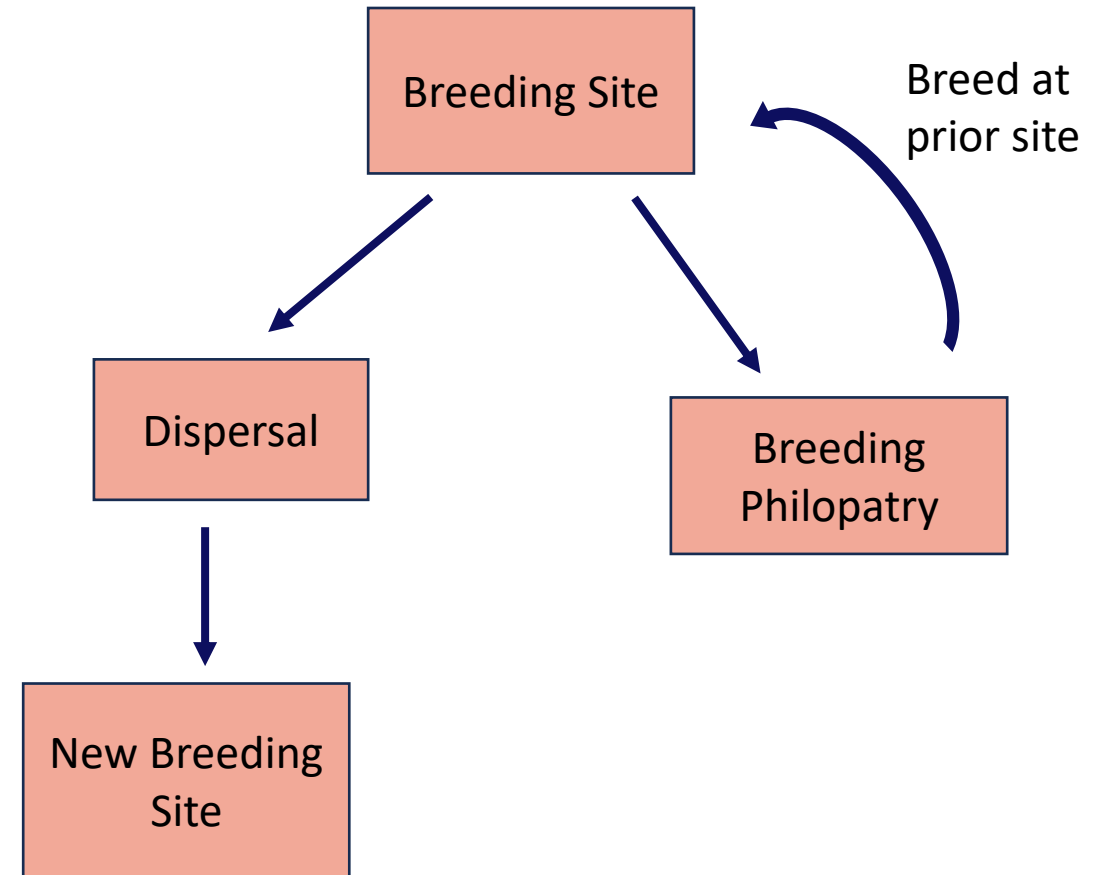


Dispersal

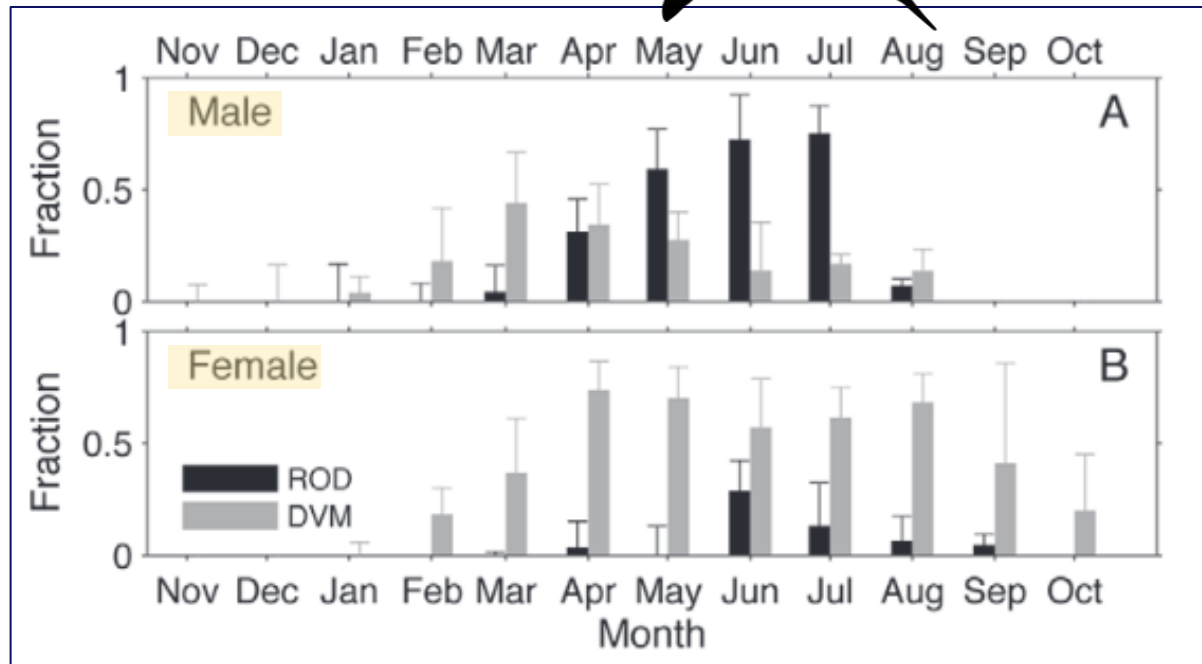
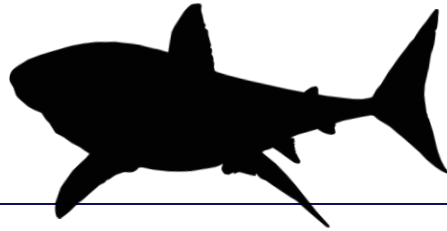
Natal Dispersal



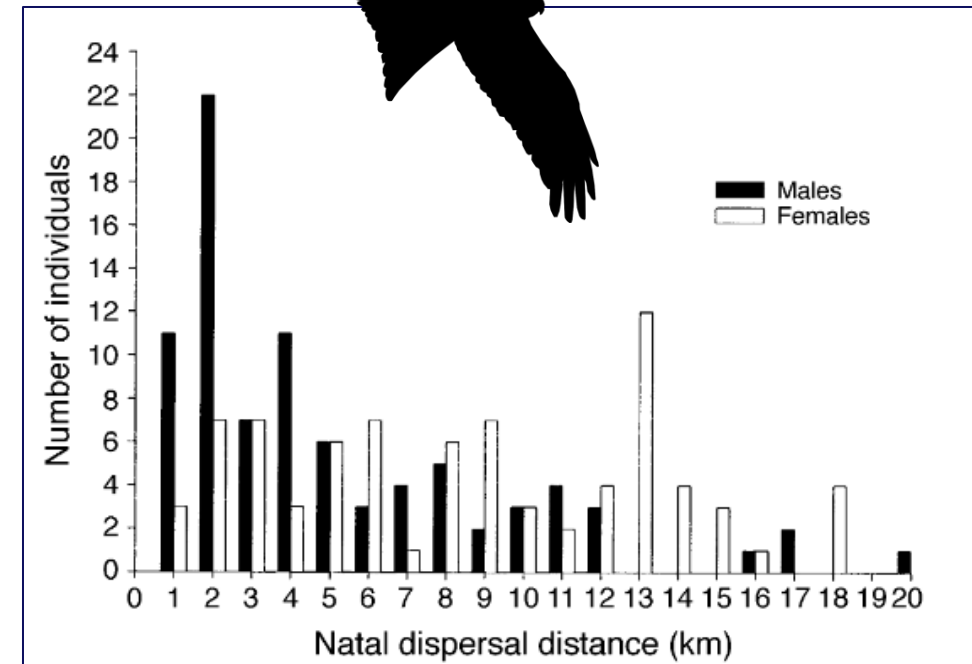
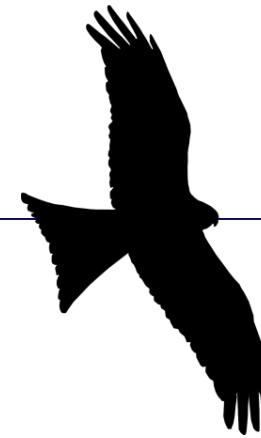
Breeding Dispersal



Sex-Biased Dispersal

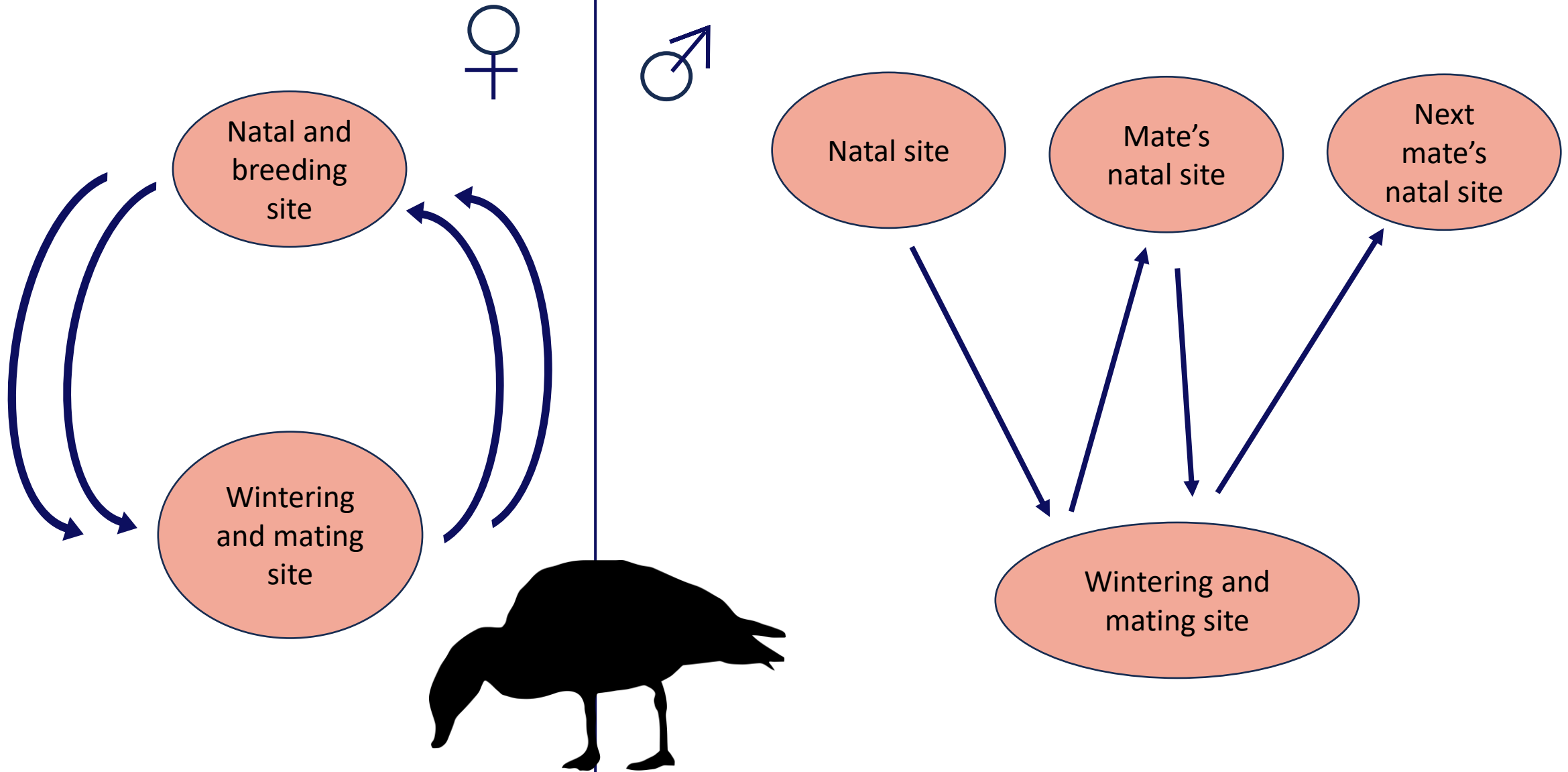


Jorgensen, S. J., et al. (2012). Eating or Meeting? Cluster Analysis Reveals Intricacies of White Shark (*Carcharodon carcharias*) Migration and Offshore Behavior. *PLoS ONE*, 7(10), e47819.

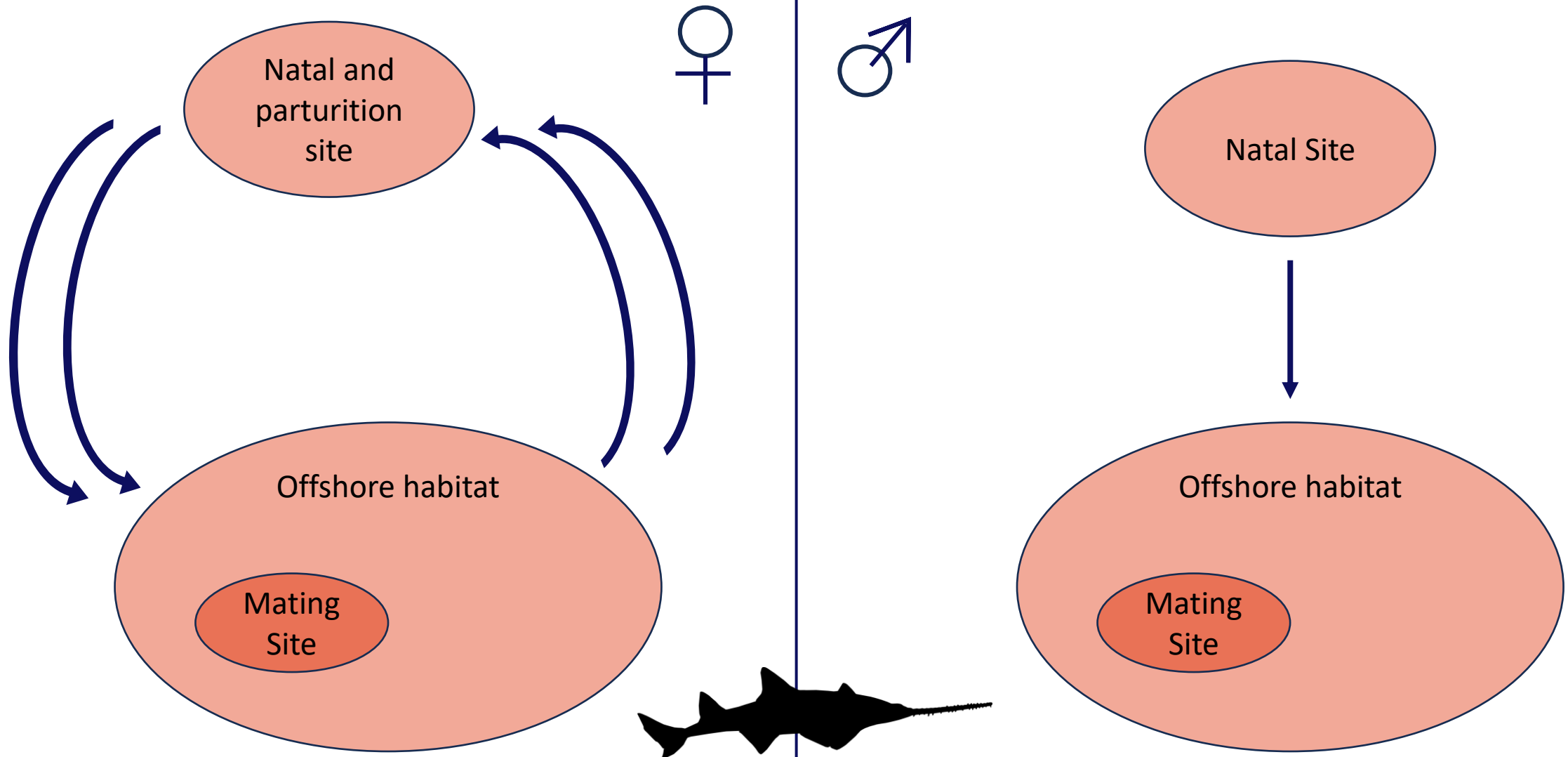


Forero, M. G., et al. (2002). Causes and Fitness Consequences of Natal Dispersal in a Population of Black Kites. *Ecology*, 83(3), 858–872.

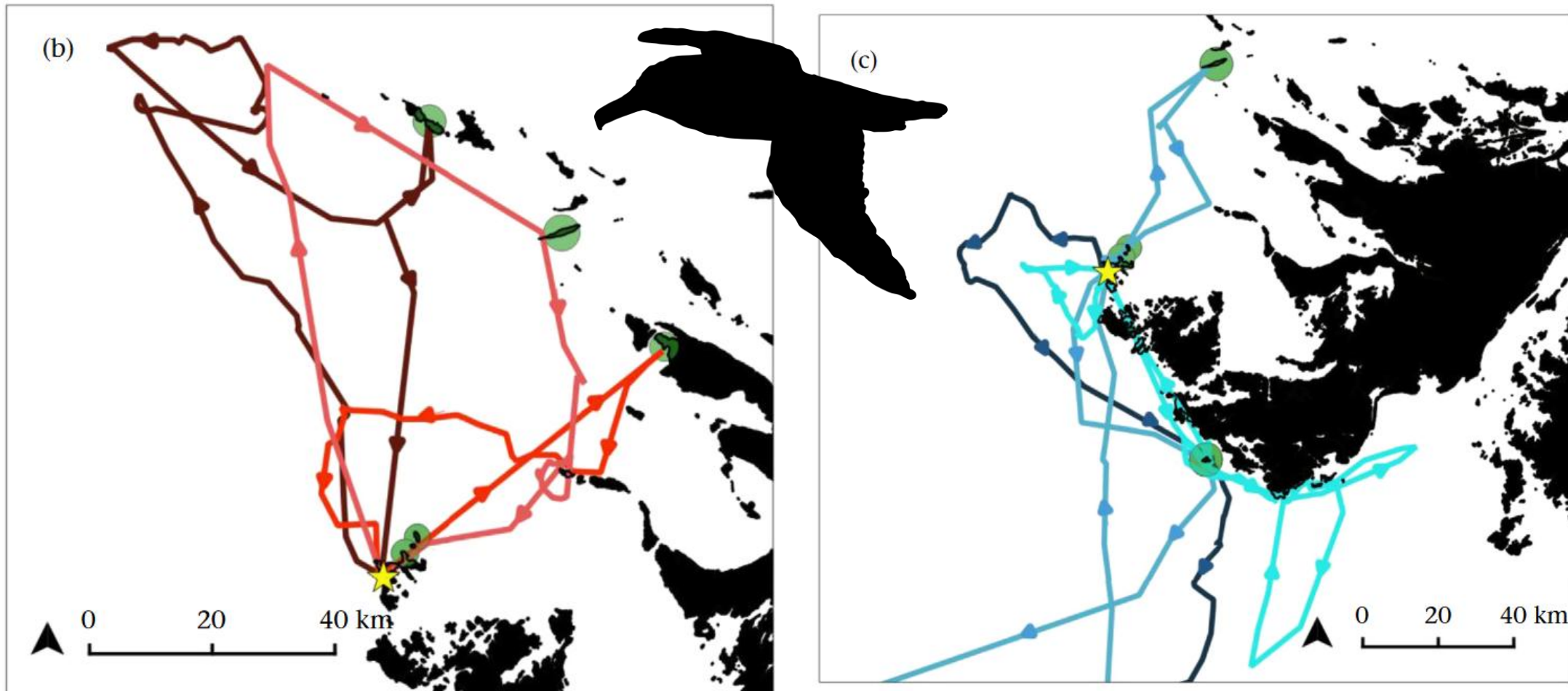
Sex-Biased Dispersal



Sex-Biased Dispersal



Dispersal: Extended Pre-breeding



Top: Campioni, L., et al. (2017). Albatrosses prospect before choosing a home: Intrinsic and extrinsic sources of variability in visit rates. *Animal Behaviour*, 128, 85–93.

Seasonal Migration and Philopatry: Various Combinations



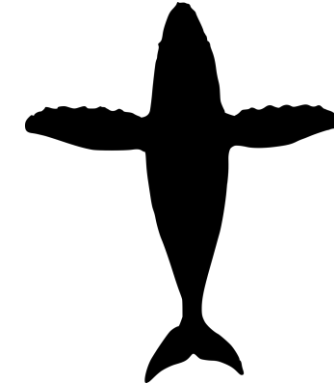
- Nomadic in breeding season
- Philopatric in winter



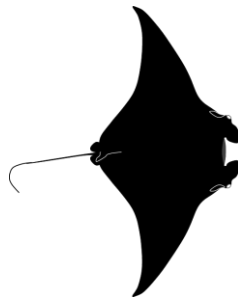
- Nomadic in breeding season
- Nomadic in winter



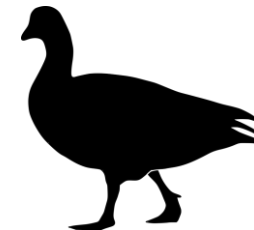
- Philopatric in breeding season
- Philopatric in winter



- Regionally philopatric in non-breeding season
- Philopatric in breeding season

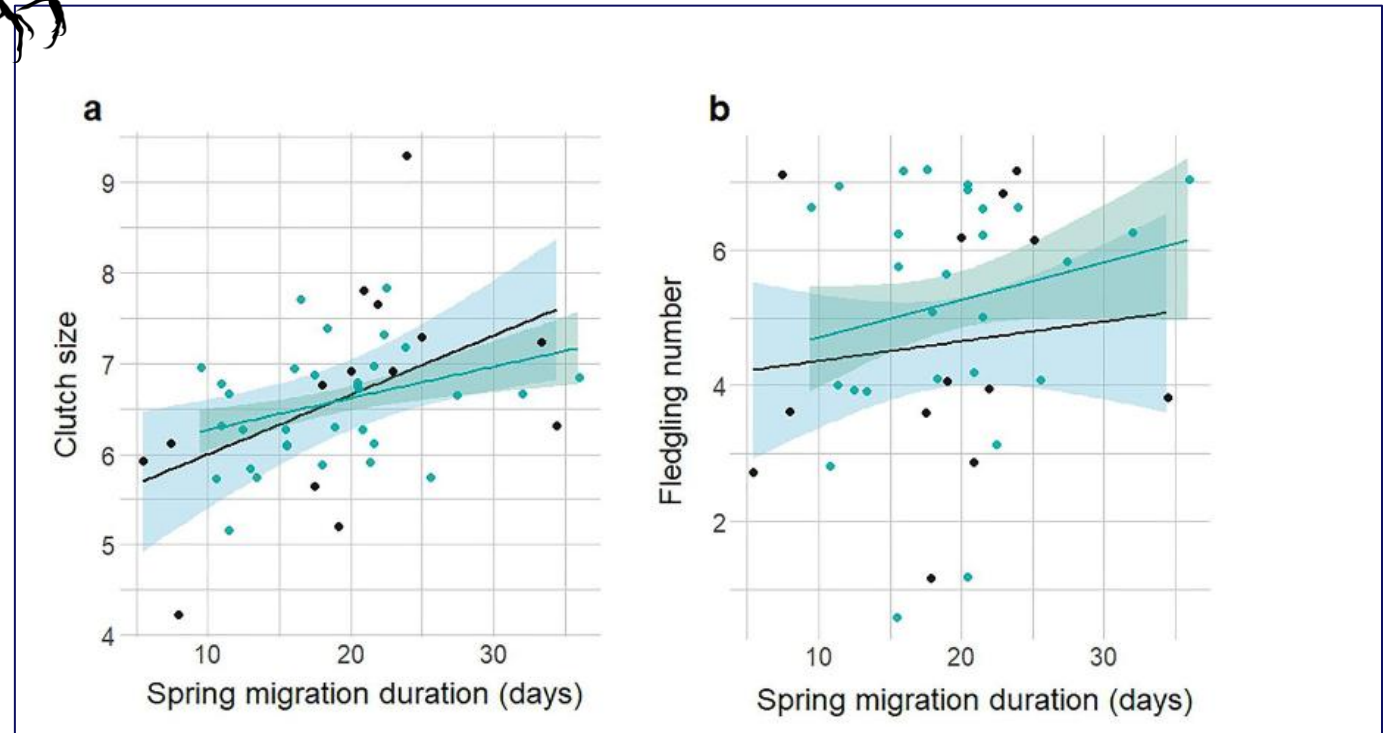
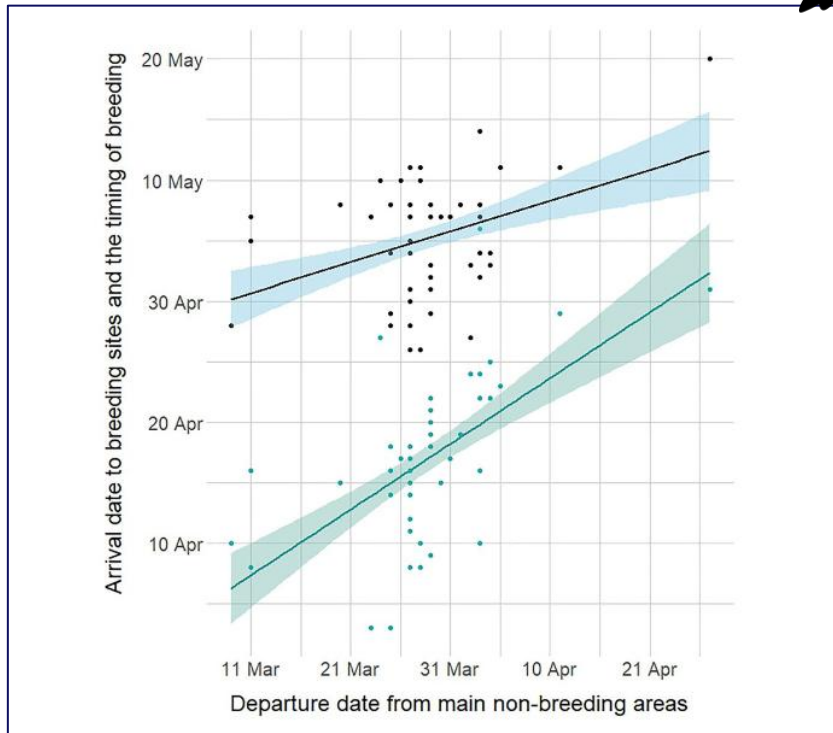
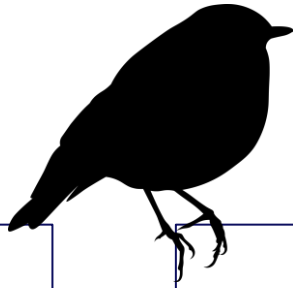


- Aggregation area philopatry



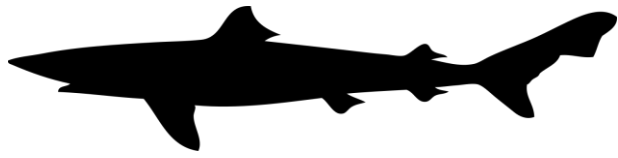
- Staging area philopatry

Seasonal Migration: Temporal Constraint and Energetic Cost

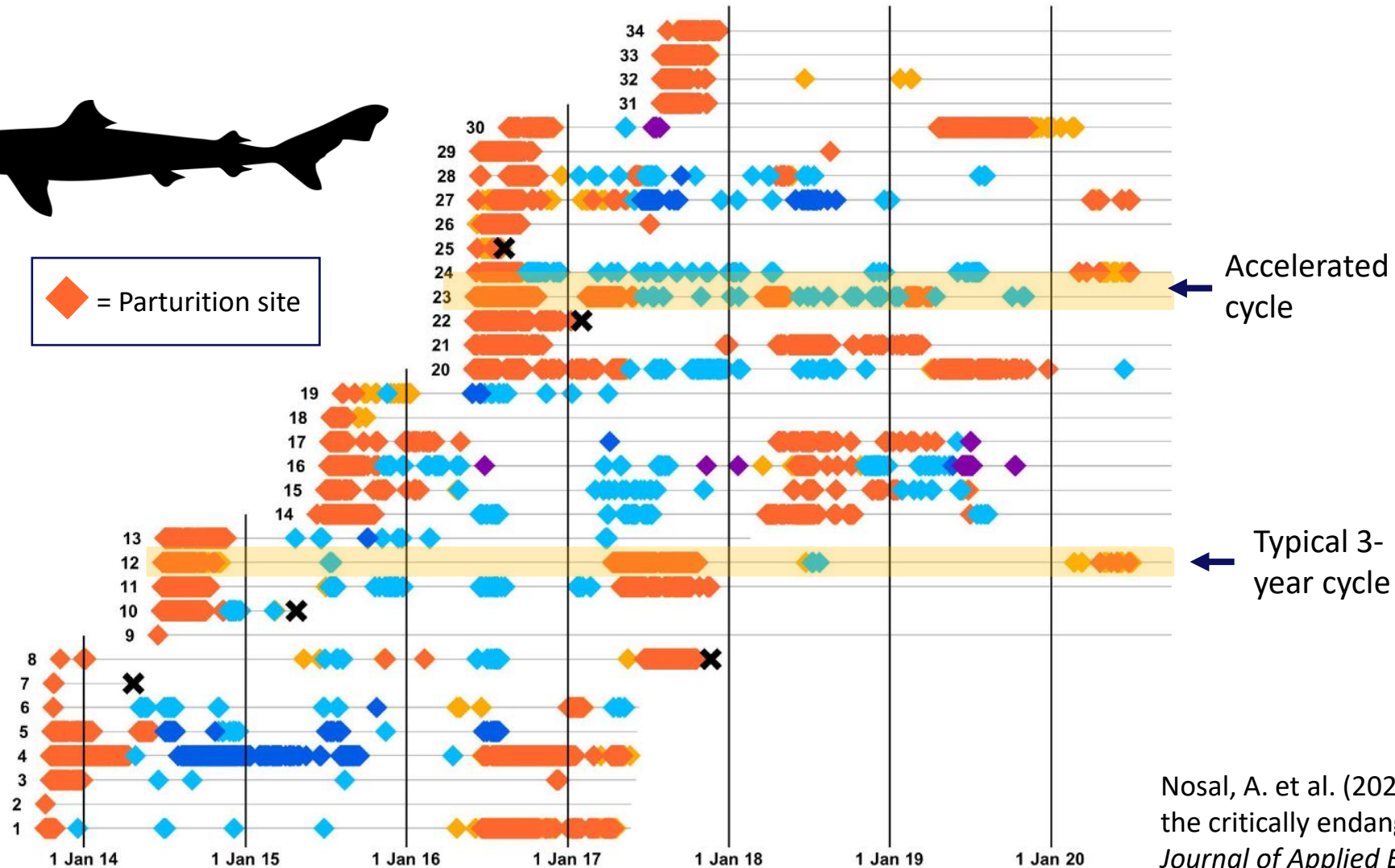


Bell, F., et al. (2024). Individuals departing non-breeding areas early achieve earlier breeding and higher breeding success. *Scientific Reports*, 14(1), 4075.

Seasonal Migration: Temporal Constraint and Energetic Cost



◆ = Parturition site



Nosal, A. et al. (2021). Triennial migration and philopatry in the critically endangered soupfin shark *Galeorhinus galeus*. *Journal of Applied Ecology*, 58(8), 1570–1582.

Seasonal Migration: Temporal Constraint and Energetic Cost

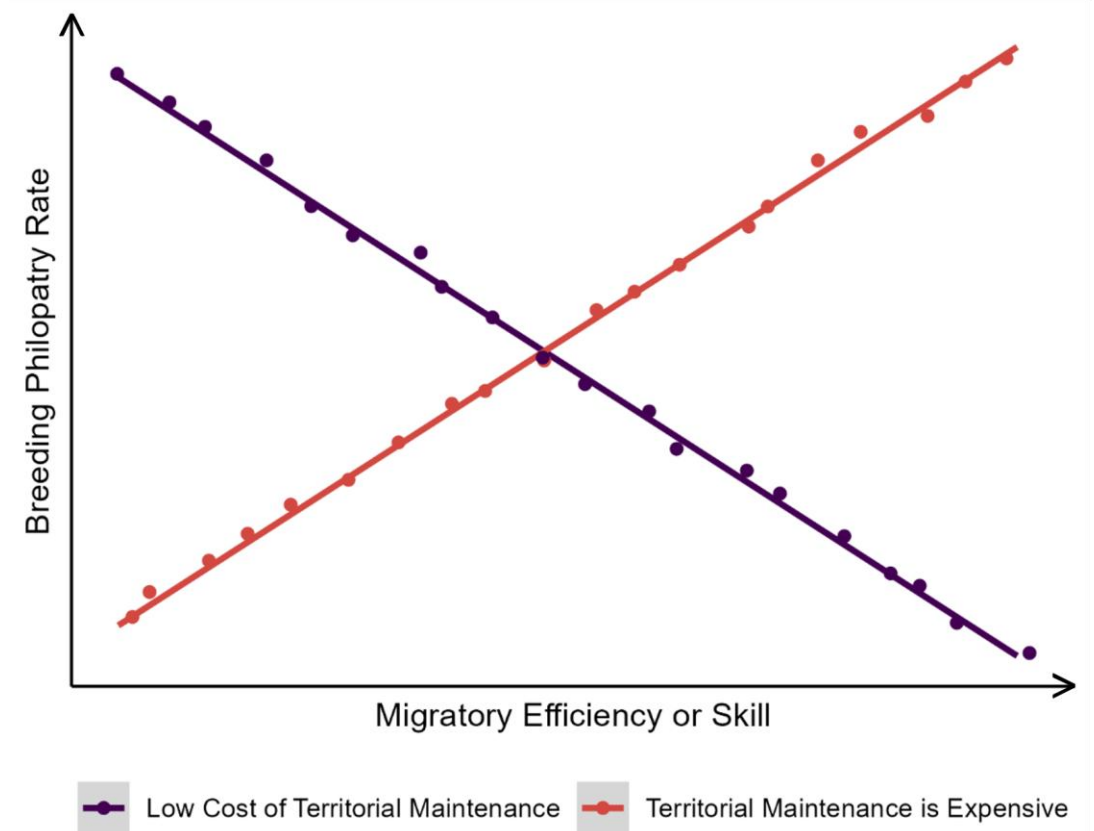
More efficient migrants might be...

More philopatric

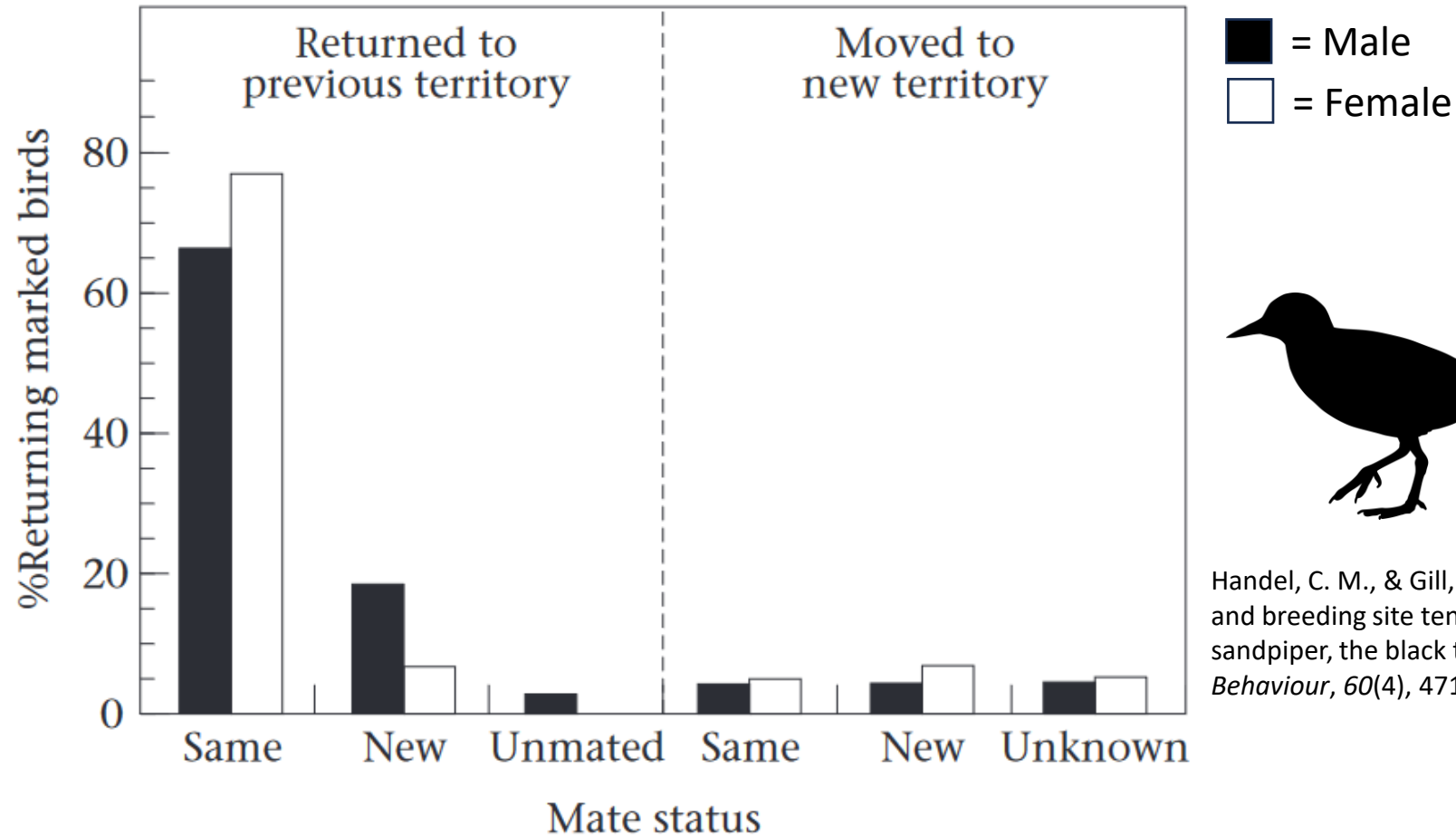
- More likely to succeed in defending preferred territory
- More likely to have the energy and time to reach their preferred site before the onset of breeding
- Able to breed (and thus return to their breeding site) more often

Less philopatric

- Able to spend time investigating new and better sites
- More likely to succeed in competing for a new and better site

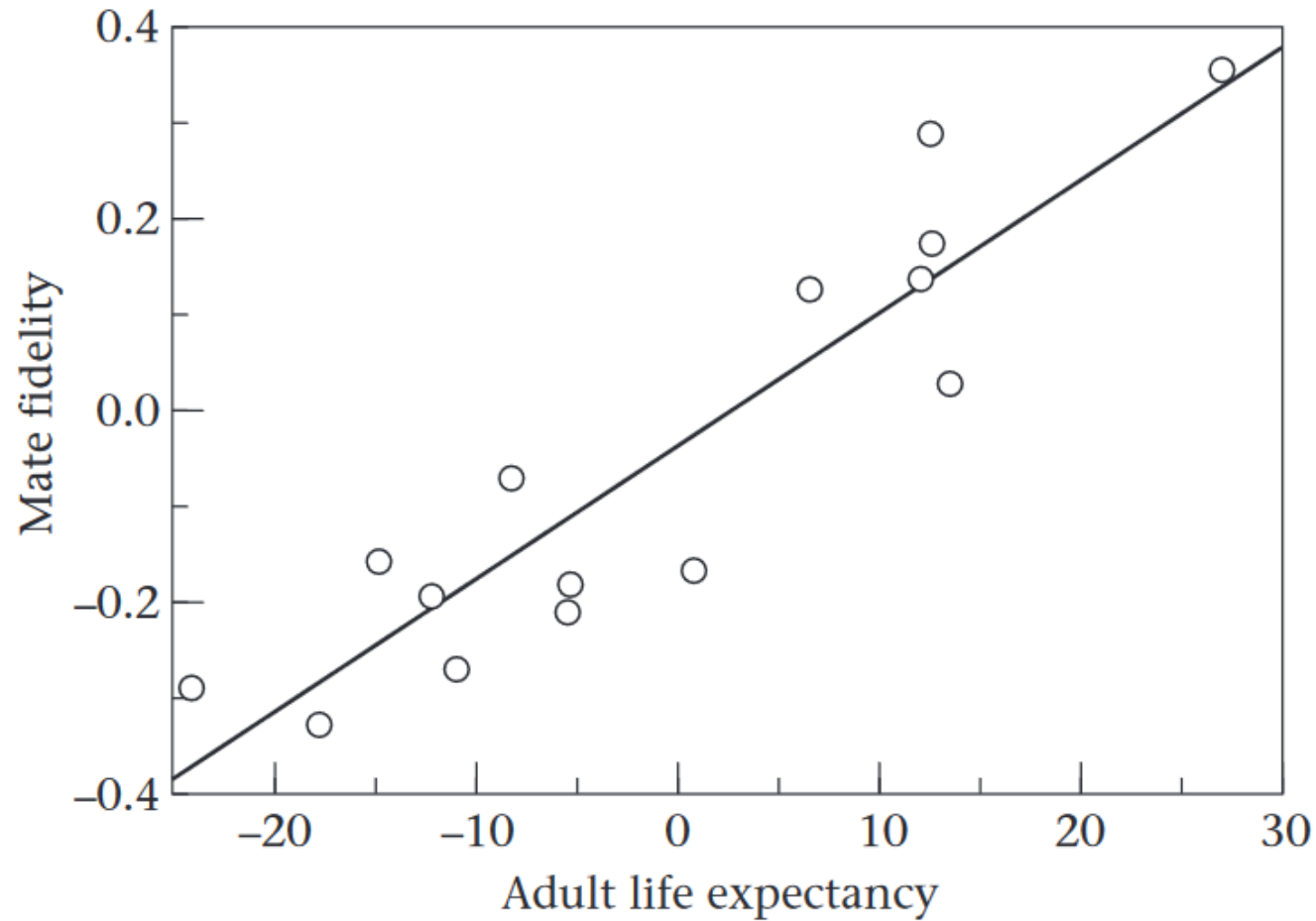


Seasonal Migration: Mate and Site Retention



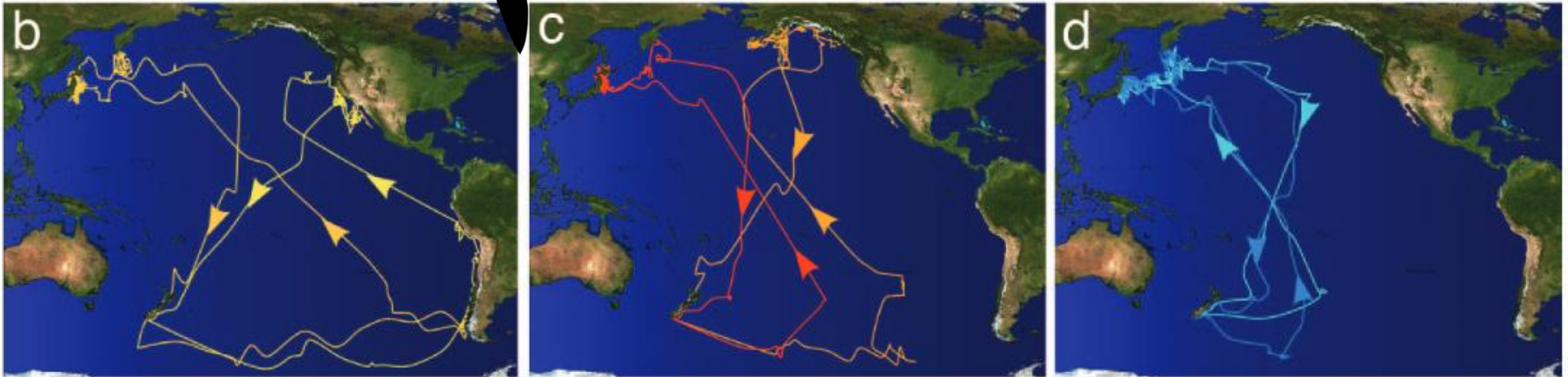
Handel, C. M., & Gill, R. E. (2000). Mate fidelity and breeding site tenacity in a monogamous sandpiper, the black turnstone. *Animal Behaviour*, 60(4), 471–481.

Seasonal Migration: Mate and Site Retention



Bried, J., et al. (2003). Mate fidelity in monogamous birds: A re-examination of the Procellariiformes. *Animal Behaviour*, 65(1), 235–246.

Seasonal Migration: Mate and Site Retention

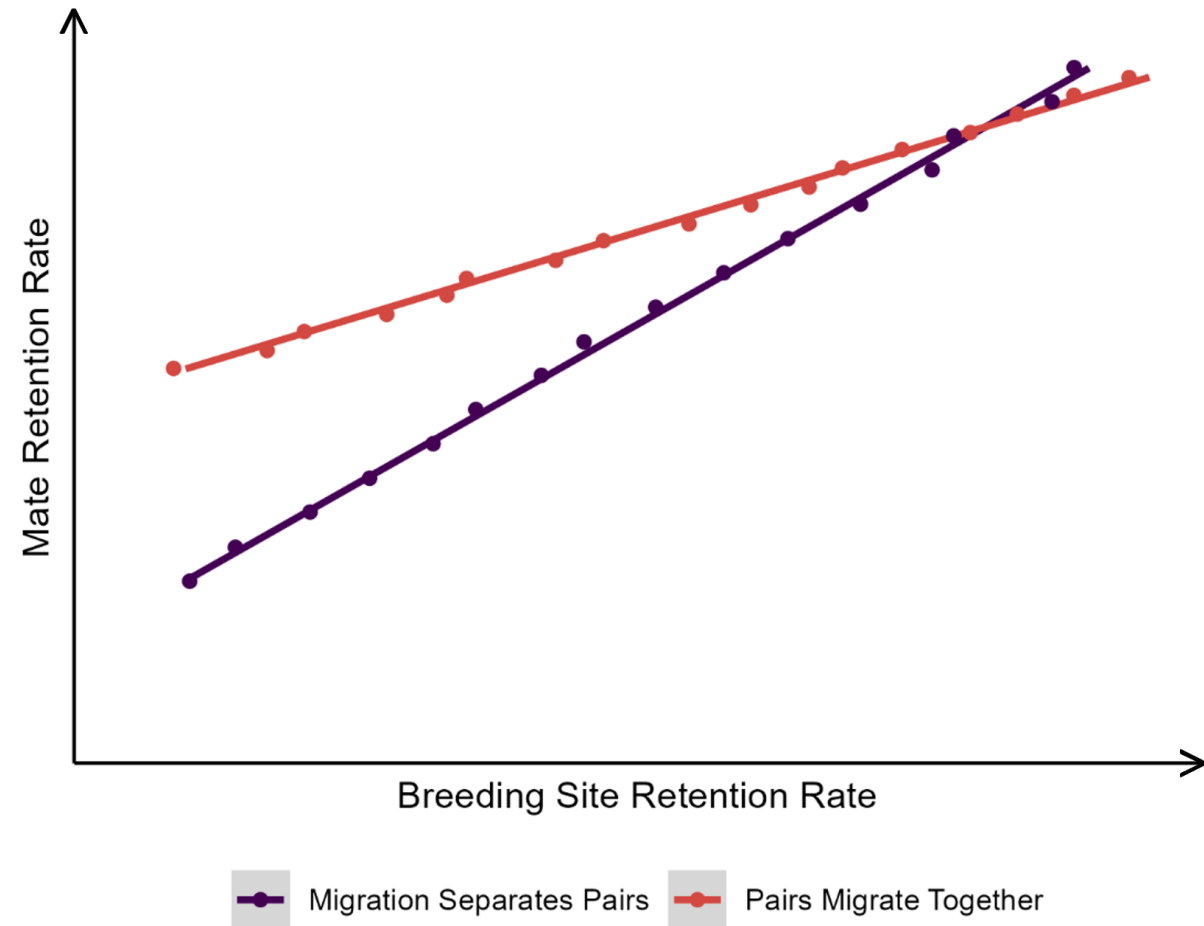


Shaffer, S. A., et al. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences*, 103(34), 12799–12802.

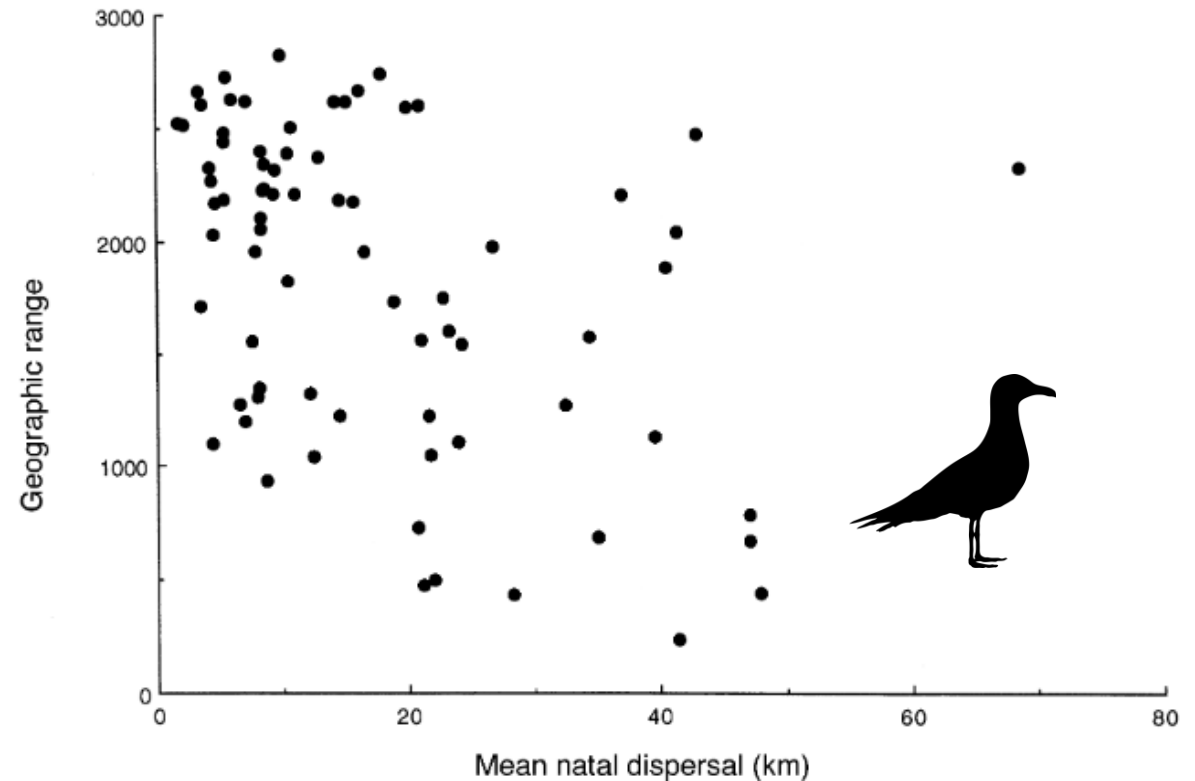
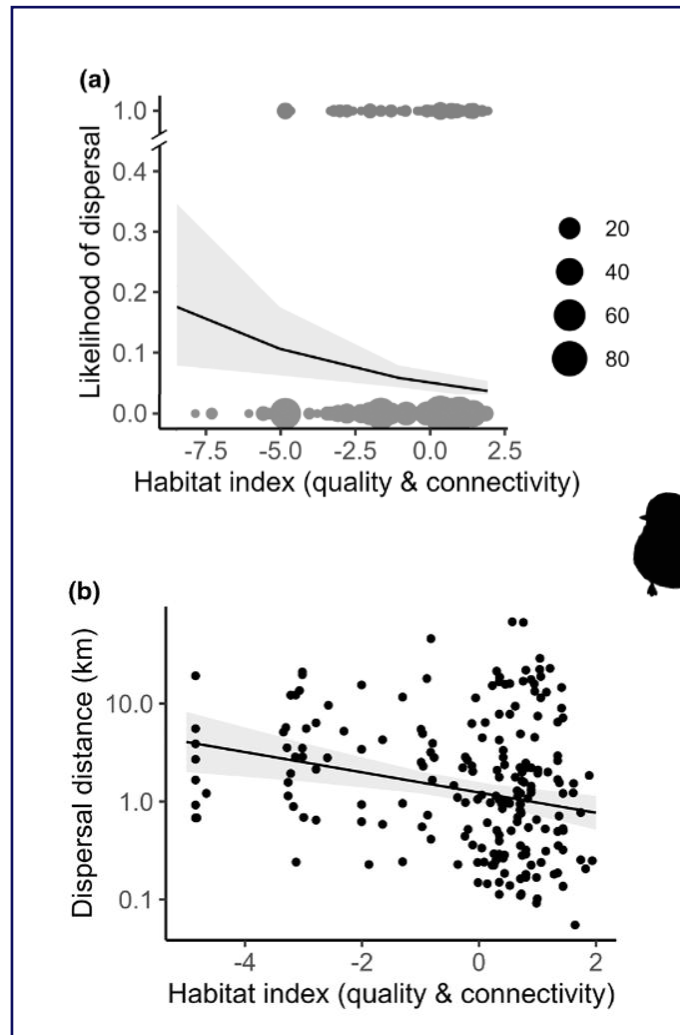
Seasonal Migration: Mate and Site Retention

Migration may influence breeding site and mate fidelity when...

- Advantages of site and mate familiarity co-occur and increase over time
- Site retention helps pairs to reunite when they are separated by migration



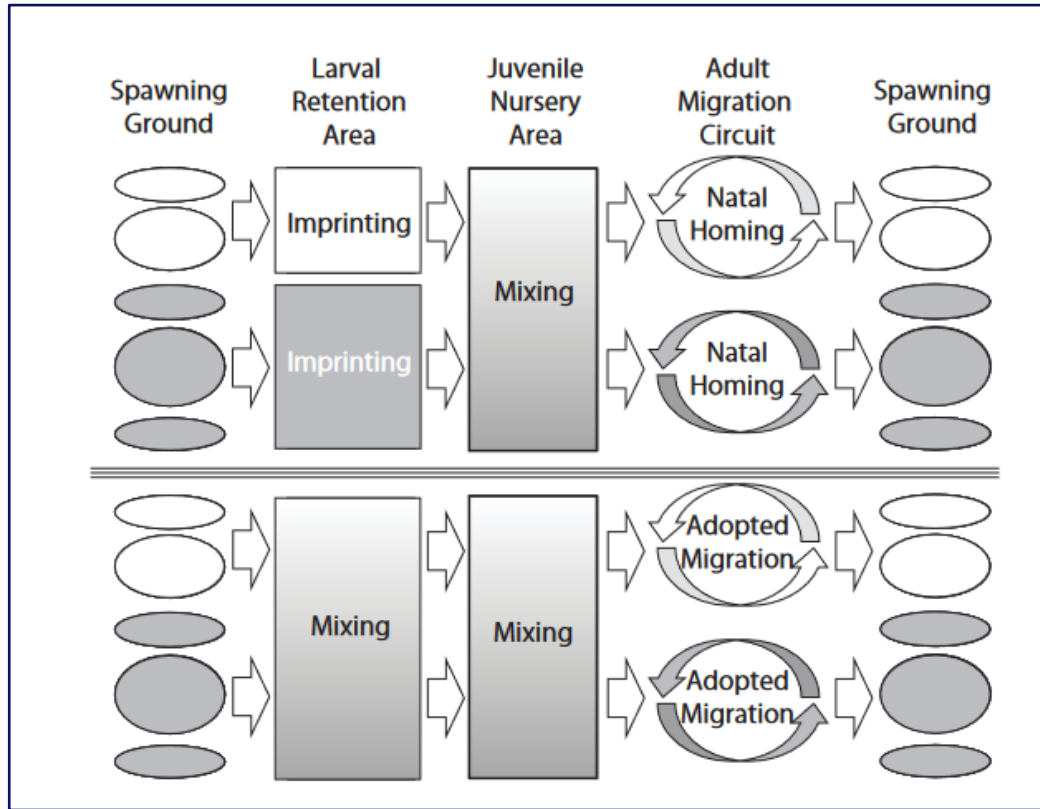
Seasonal Migration: Resource Patchiness and Predictability



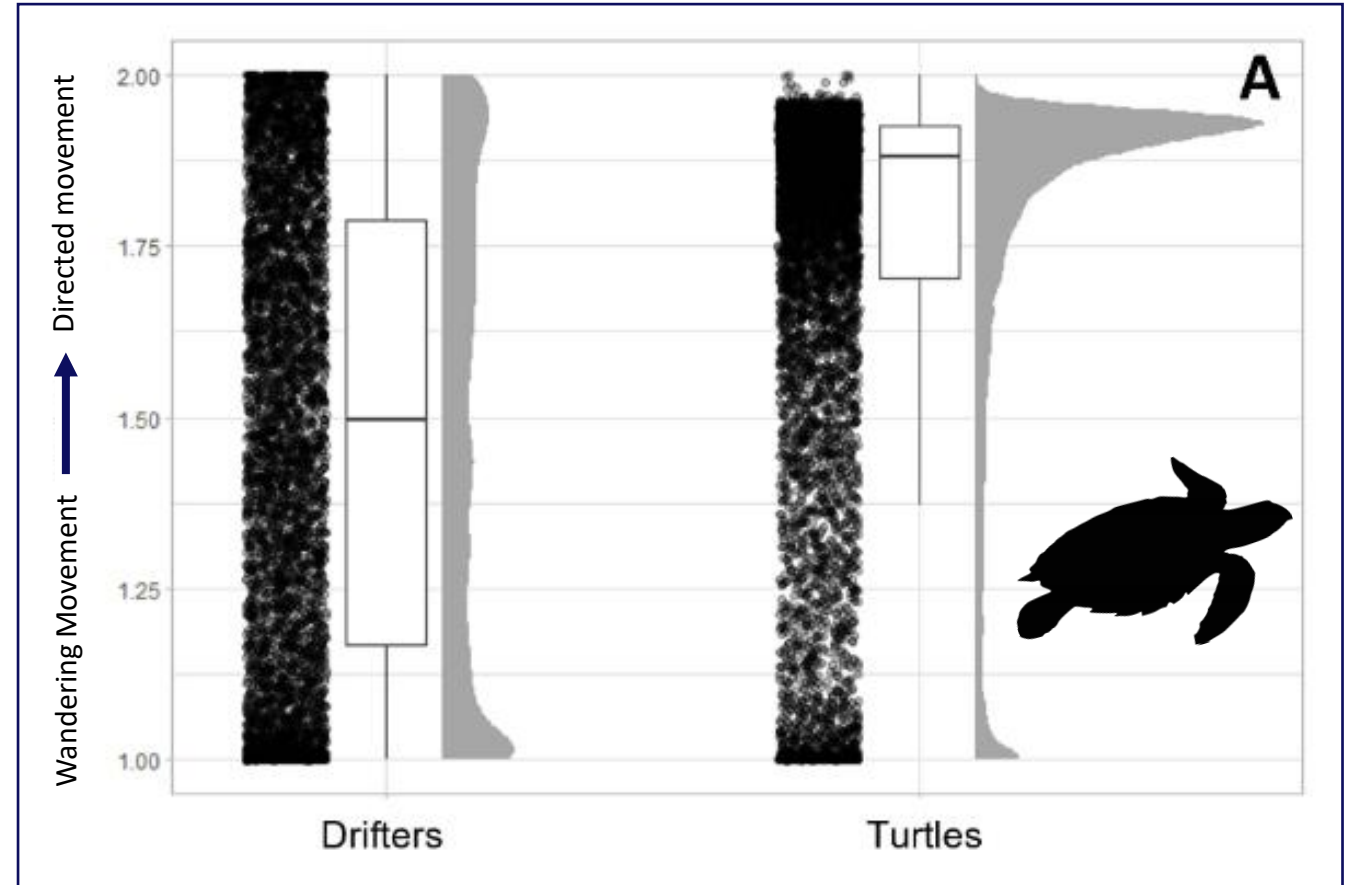
Paradis, E., et al. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, 67(4), 518–536.

Teunissen, N. et al. (2025). Climate, habitat and demography predict dispersal by an endangered bird in a fragmented landscape. *Journal of Applied Ecology*, 1365–2664.70026.

Seasonal Migration: Navigation, Vagility, and Personality



Secor, D. H. (2015). *Migration Ecology of Marine Fishes*. Johns Hopkins University Press.



Phillips, K. F., et al. (2025). New insights on sea turtle behaviour during the 'lost years.' *Proceedings of the Royal Society B: Biological Sciences*, 292(2040), 20242367.

Discussion

Species	Type
<i>Carcharias carcharius</i>	R
	SR
	SF
	RP
<i>Echinorhinus cookei</i>	R
<i>Galucarda cucier</i>	R
	SF
<i>Ginglymystoma cirratum</i>	R
	SF
<i>Heterodontus portusjacksoni</i>	R
<i>Hemachius grieco</i>	SF
	R
	SR
<i>Musculus musculus</i>	SF
	SR
	SF
<i>Negaprion aculeatus</i>	R
	SF
	R
<i>Negaprion brevirostris</i>	SF
<i>Noorynchus opedanius</i>	NP
	SR
	SF
<i>Oreochelone halei</i>	R
<i>Rhinodon typus</i>	SF
<i>Sphyrna lewini</i>	SR
	SF
	RP
	R
<i>Sphyrna tiburo</i>	SR
<i>Squalus mackleyi</i>	SF

Species	Type
<i>Carcharias carcharius</i>	R
	SR
	SF
	RP
<i>Echinorhinus cookei</i>	R
<i>Galucarda cucier</i>	R
	SF
<i>Ginglymystoma cirratum</i>	R
	SF
<i>Heterodontus portusjacksoni</i>	R
<i>Hemachius grieco</i>	SF
	SR
	SF
<i>Musculus musculus</i>	SR
	SF
	R
<i>Negaprion aculeatus</i>	SF
	R
	SF
<i>Negaprion brevirostris</i>	SF
<i>Noorynchus opedanius</i>	NP
	SR
	SF
<i>Oreochelone halei</i>	R
<i>Rhinodon typus</i>	SF
<i>Sphyrna lewini</i>	SR
	SF
	RP
	R
<i>Sphyrna tiburo</i>	SR
<i>Squalus mackleyi</i>	SF

Species	Type
<i>Carcharhinus albimarginatus</i>	R
<i>Carcharhinus amblyrhynchus</i>	R
<i>Carcharhinus ambloensis</i>	R
	RP
	SF
<i>Carcharhinus falsiformis</i>	SF
<i>Carcharhinus galapagensis</i>	R
<i>Carcharhinus leucas</i>	R
	SF
<i>Carcharhinus limbatus</i>	R
	SR
	SF
	RP
	SR
<i>Carcharhinus longimanus</i>	SR
	SF
	R
<i>Carcharhinus melanopterus</i>	R
	SF
	NP
	R
	SR
<i>Carcharhinus perezi</i>	SR
	SF
	SR
<i>Carcharhinus plumbeus</i>	SR
	SF
<i>Carcharhinus sorrah</i>	R
	SR
<i>Carcharias taurus</i>	
	SF

Common name	Species name
Townsend's meadow mouse	<i>Microtus townsendii</i>
Common vole	<i>Microtus arvalis</i>
Field vole	<i>Microtus agrestis</i>
Bank vole	<i>Clethrionomys glareolus</i>
Water vole	<i>Arvicola terrestris</i>
African wild dog	<i>Lycan pictus</i>
Red fox	<i>Vulpes vulpes</i>
Black bear	<i>Ursus americanus</i>
Coati	<i>Nasua narica</i>
Raccoon	<i>Procyon lotor</i>
Spotted hyena	<i>Crucita crocata</i>
Lion	<i>Panthera leo</i>
Southern elephant seal	<i>Mivounga leonina</i>
Weddell seal	<i>Leptonychotes weddell</i>
Alaska fur seal	<i>Callorhinus ursinus</i>
Fur seal	<i>Arctocephalus pusillus</i>
African elephant	<i>Loxodonta africana</i>
Plains zebra	<i>Equus burchelli</i>
Vicuna	<i>Vicugna vicugna</i>
Red deer	<i>Cervus elaphus</i>
White-tailed deer	<i>Odocoileus virginianus</i>
Mountain sheep	<i>Ovis canadensis</i>
Soay sheep	<i>Ovis aries</i>
Dik-dik	<i>Madoqua kirki</i>
Cape buffalo	<i>Syncerus caffer</i>

Common name	Species name
Chimpanzee	<i>Pan troglodytes</i>
Mountain gorilla	<i>Gorilla gorilla</i>
Pika	<i>Ochotona princeps</i>
Thirteen-striped ground squirrel	<i>Spermophilus tridecemlineatus</i>
Richardson's ground squirrel	<i>Spermophilus richardsonii</i>
Round-tailed ground squirrel	<i>Spermophilus tereticaudus</i>
Belding's ground squirrel	<i>Spermophilus beldingi</i>
Sonoma chipmunk	<i>Eutamias sonomae</i>
Yellow pine chipmunk	<i>Eutamias amoenus</i>
Lodgepole chipmunk	<i>Eutamias speciosus</i>
Woodchuck	<i>Marmota monax</i>
Olympic marmot	<i>Marmota olympus</i>
Yellow-bellied marmot	<i>Marmota flaviventris</i>
Black-tailed prairie dog	<i>Cynomys ludovicianus</i>
House mouse	<i>Mus musculus</i>
Wood mouse	<i>Apodemus sylvaticus</i>
Prairie deer mouse	<i>Peromyscus maniculatus</i>
Sand-rat	<i>Psamomys obesus</i>
Long-tailed pocket mouse	<i>Perognathus formosus</i>
Meadow mouse	<i>Microtus pennsylvanicus</i>
Prairie vole	<i>Microtus ochrogaster</i>

Common name	Species name
Whiptail wallaby	<i>Macropus parryi</i>
	<i>Rhynchonycteris naso</i>
White-lined bat	<i>Saccopteryx bilineata</i>
Sifaka	<i>Propithecus verreauxi</i>
Ring-tailed lemur	<i>Lemur catta</i>
Thick-tailed bushbaby	<i>Gulago crassicaudatus</i>
Howler monkey	<i>Alouatta palliata</i>
Rhesus monkey	<i>Macaca mulatta</i>
Toque monkey	<i>Macaca sinica</i>
Japanese macaque	<i>Macaca fuscata</i>
Vorvet monkey	<i>Cercopithecus aethiops</i>
Black-and-white colobus	<i>Colobus guereza</i>
Patas monkey	<i>Erythrocebus patas</i>
Chacma baboon	<i>Papio ursinus</i>
Olive baboon	<i>Papio anubis</i>
Yellow baboon	<i>Papio cynocephalus</i>
Hamadryas baboon	<i>Papio hamadryas</i>
Gelada baboon	<i>Theropithecus gelada</i>
Nilgiri langur	<i>Presbytis johnii</i>
Purple-faced langur	<i>Presbytis senex</i>
Hanuman langur	<i>Presbytis entellus</i>
Lar gibbon	<i>Hylobates lar</i>
Orang-utan	<i>Pongo pygmaeus</i>

Species	Species
<i>Dendrocygna bicolor</i>	<i>Chen caerulescens</i>
<i>Chen caerulescens</i>	<i>Branta canadensis</i>
<i>Chen caerulescens</i>	<i>Anas clypeata</i>
<i>Branta canadensis</i>	<i>A. strepera</i>
	<i>A. acuta</i> ^a
Same mate	<i>A. americana</i>
New mate	<i>Aythya affinis</i>
<i>Anas strepera</i>	<i>A. valisineria</i>
<i>A. clypeata</i>	<i>A. collaris</i>
<i>A. platyrhynchos</i>	<i>A. ferina</i>
<i>A. americana</i>	<i>A. platyrhynchos</i>
<i>Aythya affinis</i>	<i>A. strepera</i>
<i>A. valisineria</i>	<i>A. valisineria</i>
<i>A. collaris</i>	<i>A. collaris</i>
<i>A. ferina</i>	<i>A. ferina</i>
<i>A. fuligula</i>	<i>A. fuligula</i>
<i>Histrionicus histrionicus</i>	<i>Tadorna variegata</i>
	<i>T. tadornoides</i>
	<i>T. tadorna</i>
Same estuary	<i>Aix sponsa</i> ^a
<i>T. tadornoides</i>	<i>Somateria mollissima</i>
<i>T. variegata</i>	
<i>Aix sponsa</i> ^a	
<i>Chenonetta jubata</i>	

Species	Species
<i>A. affinis</i>	<i>Anas americana</i>
	<i>A. platyrhynchos</i>
<i>A. fuligula</i>	
<i>A. ferina</i>	
<i>Aix sponsa</i>	
<i>Clangula hyemalis</i>	<i>A. acuta</i>
<i>Somateria mollissima</i>	<i>A. strepera</i>
<i>Histrionicus histrionicus</i>	
<i>Melanitta fusca</i>	
<i>Bucephala clangula</i>	
<i>Clangula hyemalis</i>	
<i>Tadorna tadorna</i>	<i>A. quereedula</i>
Previous territory	<i>Aythya collaris</i>
Same estuary	
<i>T. tadornoides</i>	
<i>T. variegata</i>	
<i>Aix sponsa</i> ^a	
<i>Chenonetta jubata</i>	

Species
<i>Pristis pectinata</i>
<i>Aetobatus narinari</i>
<i>Pristis pristis</i>
<i>Pristis zijsron</i>
<i>Raja brachyura</i>
<i>Raja microocellata</i>
<i>Raja undulata</i>
<i>Rhinobatos productus</i>
<i>Rhinoptera bonasus</i>
<i>Rhynchobatus</i> spp.
<i>Urobatis halleri</i>
<i>Urogymnus asperrimu</i>
<i>Zapteryx exasperata</i>
<i>Himantura dalyensis</i>

Common Name	Scientific Name
Common Eider	<i>Somateria mollissima</i>
Manx Shearwater	<i>Puffinus puffinus</i>
Northern Fulmar	<i>Fulmarus glacialis</i>
Great Skua	<i>Stercorarius skua</i>
Arctic Skua	<i>Stercorarius parasiticus</i>
Common Guillemot	<i>Uria aulge</i>
Razorbill	<i>Alca torda</i>
Atlantic Puffin	<i>Fratercula arctica</i>
Black-legged Kittiwake	<i>Rissa tridactyla</i>
Black-headed Gull	<i>Chroicocephalus ridibundus</i>
Herring Gull	<i>Larus argentatus</i>
Least Tern	<i>Sterna antillarum</i>
Common Tern	<i>Sterna hirundo</i>
Common Name	Scientific Name
Canada Goose (U.K.)	<i>Branta canadensis</i>
Mute Swan	<i>Cygnus olor</i>
Mallard	<i>Anas platyrhynchos</i>
White Stork	<i>Ciconia ciconia</i>
Whooping Crane	<i>Grus americana</i>
Greater Flamingo	<i>Phoenicopterus roseus</i>
Northern Lapwing	<i>Vanellus vanellus</i>
Ringed Plover	<i>Charadrius hiaticula</i>
Redshank	<i>Tringa totanus</i>
Black-tailed Godwit	<i>Limosa limosa</i>
Common Sandpiper	<i>Actitis hypoleucos</i>
Dunlin	<i>Calidris alpina</i>
White-throated Dipper	<i>Cinclus cinclus</i>
<i>Himantura dalyensis</i>	
<i>Himantura fai</i>	
<i>Himantura granulata</i>	
<i>Himantura uarnak</i>	
<i>Malacoraja clavata</i>	
<i>Manta alfredi</i>	
<i>Myliobatis californica</i>	
<i>Neotrygon kuhlii</i>	
<i>Paratrygon ajereba</i>	
<i>Pastinachus atrus</i>	
<i>Pristis clavata</i>	
<i>Manta birostris</i>	

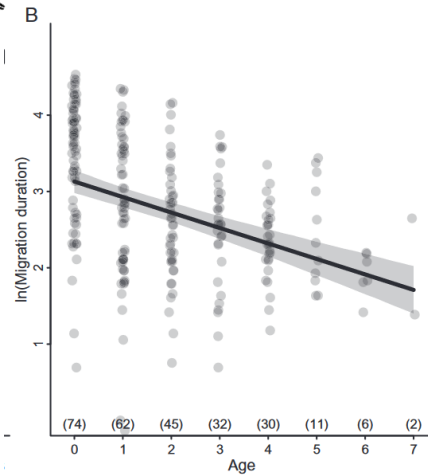
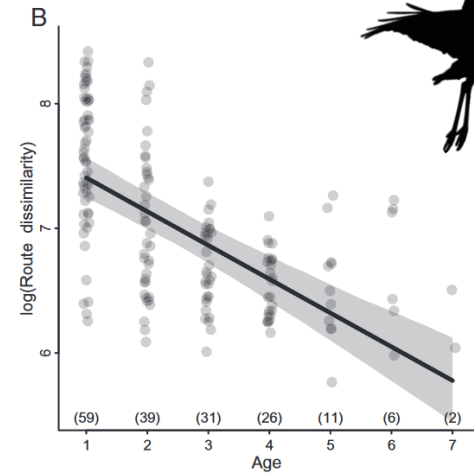
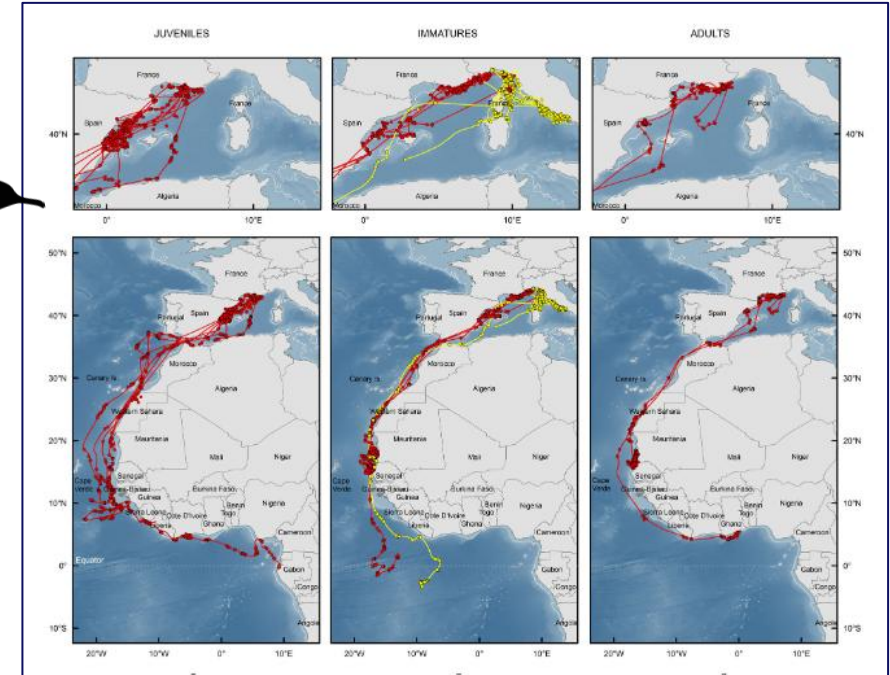
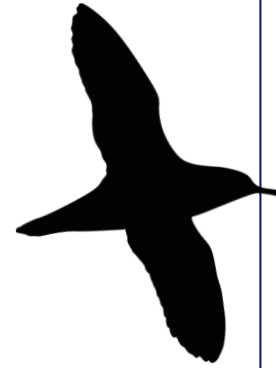
Common Name	Scientific Name
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<i>Neotrygon kuhlii</i>	
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*Sources on slide 41

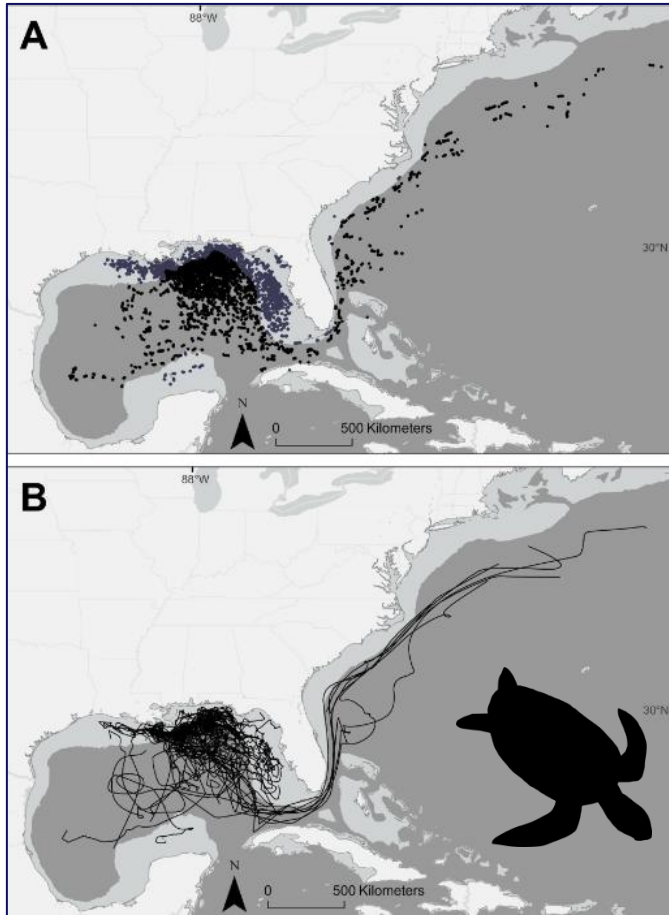
Discussion



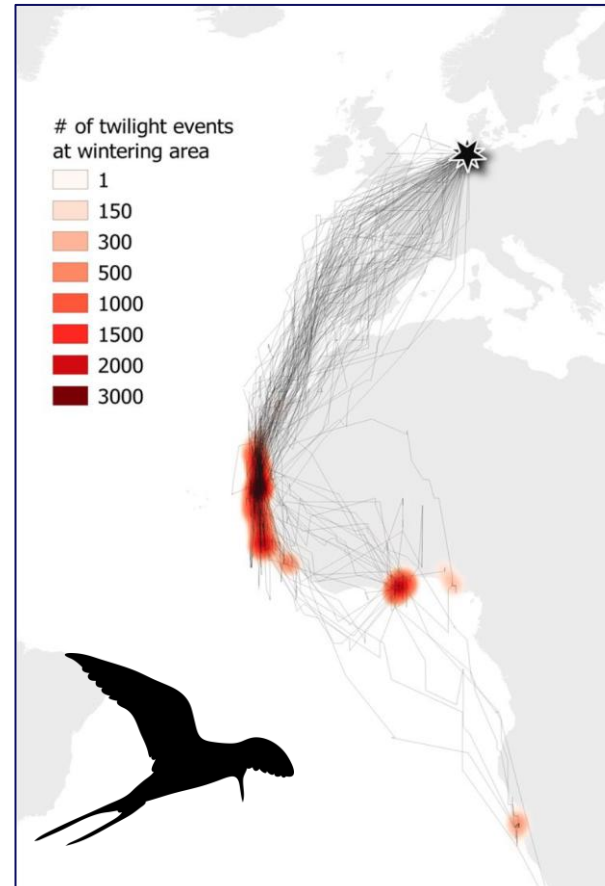
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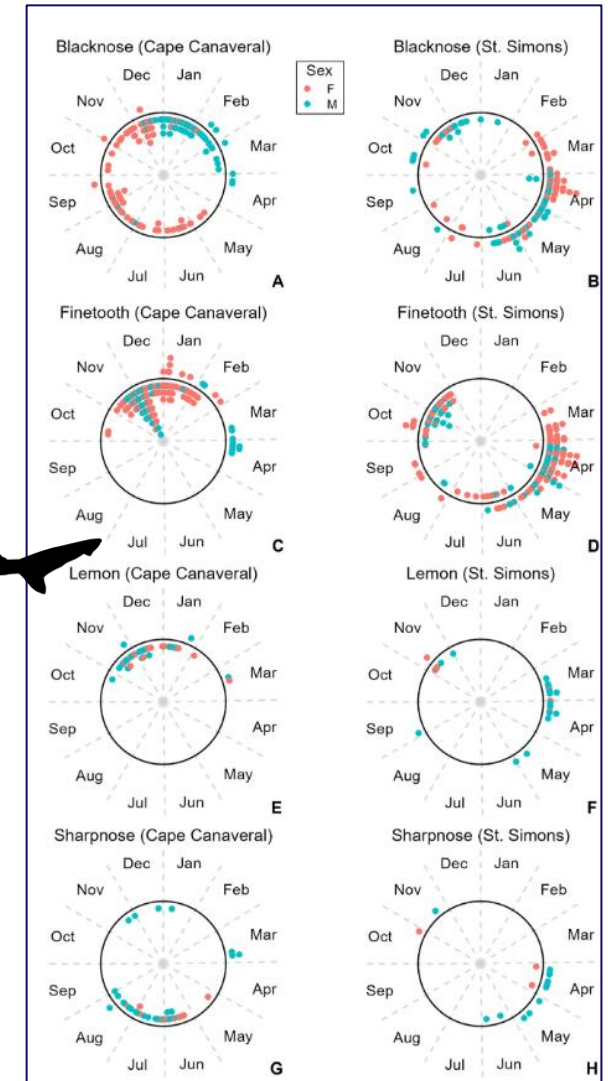
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Image Sources

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- African oystercatcher: <https://macaulaylibrary.org/asset/632840506> and <https://macaulaylibrary.org/asset/205718161>
- Soupfin shark: <https://www.montereybayaquarium.org/animals/animals-a-to-z/soupfin-shark>
- Hawksbill: <https://www.fisheries.noaa.gov/species/hawksbill-turtle>
- Humpback whale: <https://hawaiihumpbackwhale.noaa.gov/>
- Steelhead: https://www.aquariumofpacific.org/onlinelearningcenter/species/southern_california_steelhead
- All silhouettes from www.phylopic.org and are free of usage restrictions.

...And special thanks to friends who generously lent photos: Wriley Hodge, Jill Taylor

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Appendix: “Long-lived”



~25 years



200+ years



~50 years



~5 years

Variable	Definition	Bounds	Example values
r	Population growth rate (“fitness”)		
x	Age	≥ 0	
α	Age at first reproduction	≥ 0	1, 2, ..., 8
ω	Age at last reproduction	$\geq \alpha$	30
B_x	Offspring produced at age x	≥ 0	
L_x	Survivorship to age x	$\geq 0, < 1$	
b	Annual fecundity (static)	≥ 0	1.00
d	Fecundity growth rate (linear)	≥ 0	0.15
g	Fecundity growth rate (von Bertalanffy)	≥ 0	0.10
F	Fecundity maximum (von Bertalanffy)	≥ 0	2.00
S	Survival rate (static)	$\geq 0, < 1$	0.80
j	Juvenile survival rate	$\geq 0, < 1$	0.95
s	Adult survival rate	$\geq 0, < 1$	0.80

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