

## **Ecological insights from three decades of animal movement tracking across a changing Arctic**

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### **Title: Ecological insights from three decades of animal movement tracking across a changing Arctic**

Authors: Sarah C. Davidson<sup>1,2,3</sup>, Gil Bohrer<sup>1\*</sup>, Eliezer Gurarie<sup>4,5</sup>, Scott LaPoint<sup>2,6,7</sup>, Peter J. Mahoney<sup>8</sup>, Natalie T. Boelman<sup>7</sup>, Jan U.H. Eitel<sup>9</sup>, Laura R. Prugh<sup>8</sup>, Lee A. Vierling<sup>9</sup>, Jyoti 5 Jennewein<sup>9</sup>, Emma Grier<sup>4</sup>, Ophélie Couriot<sup>4,10</sup>, Allicia P. Kelly<sup>11</sup>, Arjan J.H. Meddens<sup>12</sup>, Ruth Y. Oliver<sup>7,13,14</sup>, Roland Kays<sup>15</sup>, Martin Wikelski<sup>2,3</sup>, Tomas Aarvak<sup>16</sup>, Joshua T. Ackerman<sup>17</sup>, José A. Alves<sup>18,19</sup>, Erin Bayne<sup>20</sup>, Bryan Bedrosian<sup>21</sup>, Jerrold L. Belant<sup>22</sup>, Andrew M. Berdahl<sup>23</sup>, Alicia M. Berlin<sup>24</sup>, Dominique Berteaux<sup>25</sup>, Joël Bêty<sup>25</sup>, Dmitrijs Boiko<sup>26,27,28</sup>, Travis L. Booms<sup>29</sup>, Bridget L. Borg<sup>30</sup>, Stan Boutin<sup>20</sup>, W. Sean Boyd<sup>31</sup>, Kane Brides<sup>32</sup>, Stephen Brown<sup>33</sup>, Victor N. Bulyuk<sup>34</sup>, 10 Kurt K. Burnham<sup>35</sup>, David Cabot<sup>36</sup>, Michael Casazza<sup>17</sup>, Katherine Christie<sup>37</sup>, Erica H. Craig<sup>38</sup>, Shanti E. Davis<sup>39</sup>, Tracy Davison<sup>40</sup>, Dominic Demma<sup>41</sup>, Christopher R. DeSorbo<sup>42</sup>, Andrew Dixon<sup>43</sup>, Robert Domenech<sup>44</sup>, Götz Eichhorn<sup>45,46</sup>, Kyle Elliott<sup>47</sup>, Joseph R. Evenson<sup>48</sup>, Klaus-Michael Exo<sup>49</sup>, Steven H. Ferguson<sup>50</sup>, Wolfgang Fiedler<sup>2,3</sup>, Aaron Fisk<sup>51</sup>, Jérôme Fort<sup>52</sup>, Alastair Franke<sup>20,53</sup>, Mark R. Fuller<sup>54</sup>, Stefan Garthe<sup>55</sup>, Gilles Gauthier<sup>56</sup>, Grant Gilchrist<sup>57</sup>, Petr Glazov<sup>58</sup>, 15 Carrie E. Gray<sup>59</sup>, David Grémillet<sup>60,61</sup>, Larry Griffin<sup>32</sup>, Mike Hallworth<sup>62,63</sup>, Autumn-Lynn Harrison<sup>62</sup>, Holly L. Hennin<sup>31,64</sup>, J. Mark Hipfner<sup>65</sup>, James Hodson<sup>66</sup>, James A. Johnson<sup>67</sup>, Kyle Joly<sup>68</sup>, Kimberly Jones<sup>41</sup>, Todd E. Katzner<sup>69</sup>, Jeff W. Kidd<sup>70</sup>, Elly C. Knight<sup>20</sup>, Michael N. Kochert<sup>69</sup>, Andrea Kölzsch<sup>2,3,71</sup>, Helmut Kruckenberg<sup>71</sup>, Benjamin J. Lagassé<sup>72</sup>, Sandra Lai<sup>25</sup>, Jean-François Lamarre<sup>73</sup>, Richard B. Lanctot<sup>67</sup>, Nicholas C. Larter<sup>74</sup>, A. David M. Latham<sup>20,75</sup>, 20 Christopher J. Latty<sup>76</sup>, James P. Lawler<sup>77</sup>, Don-Jean Léandri-Breton<sup>25</sup>, Hansoo Lee<sup>78</sup>, Stephen B. Lewis<sup>79</sup>, Oliver P. Love<sup>64</sup>, Jesper Madsen<sup>80</sup>, Mark Maftei<sup>39</sup>, Mark L. Mallory<sup>81</sup>, Buck Mangipane<sup>82</sup>, Mikhail Y. Markovets<sup>34</sup>, Peter P. Marra<sup>83</sup>, Rebecca McGuire<sup>84</sup>, Carol L. McIntyre<sup>30</sup>, Emily A. McKinnon<sup>85</sup>, Tricia A. Miller<sup>86,87</sup>, Sander Moonen<sup>49</sup>, Tong Mu<sup>88</sup>, Gerhard J.D.M. Müskens<sup>89</sup>, Janet Ng<sup>20</sup>, Kerry L. Nicholson<sup>29</sup>, Ingar Jostein Øien<sup>16</sup>, Cory Overton<sup>17</sup>, 25 Patricia A. Owen<sup>30</sup>, Allison Patterson<sup>47</sup>, Aevar Petersen<sup>90</sup>, Ivan Pokrovsky<sup>2,91,92</sup>, Luke L. Powell<sup>62,93,94</sup>, Rui Prieto<sup>95</sup>, Petra Quillfeldt<sup>96</sup>, Jennie Rausch<sup>97</sup>, Kelsey Russell<sup>98</sup>, Sarah T. Saalfeld<sup>67</sup>, Hans Schekkerman<sup>99</sup>, Joel A. Schmutz<sup>100</sup>, Philipp Schwemmer<sup>55</sup>, Dale R. Seip<sup>101</sup>, Adam Shreading<sup>44</sup>, Mónica A. Silva<sup>95,102</sup>, Bryan W. Smith<sup>103</sup>, Fletcher Smith<sup>104</sup>, Jeff P. Smith<sup>105,106</sup>, Katherine R.S. Snell<sup>107</sup>, Aleksandr Sokolov<sup>92</sup>, Vasiliy Sokolov<sup>108</sup>, Diana V 30 Solovyeva<sup>91</sup>, Mathew S. Sorum<sup>109</sup>, Grigori Tertitski<sup>58</sup>, J.F. Therrien<sup>56,110</sup>, Kasper Thorup<sup>107</sup>, T. Lee Tibbitts<sup>100</sup>, Ingrid Tulp<sup>109</sup>, Brian D. Uher-Koch<sup>100</sup>, Rob S.A. van Bemmelen<sup>111,112</sup>, Steven Van Wilgenburg<sup>113</sup>, Andrew L. Von Duyke<sup>114</sup>, Jesse L. Watson<sup>20</sup>, Bryan D. Watts<sup>104</sup>, Judy A. Williams<sup>66</sup>, Matthew T. Wilson<sup>48</sup>, Jay Wright<sup>115</sup>, Michael A. Yates<sup>116</sup>, David J. Yurkowski<sup>50,85</sup>, Ramūnas Žydelis<sup>117</sup>, Mark Hebblewhite<sup>5</sup>

#### 35 **Affiliations:**

<sup>1</sup> Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, Columbus, OH, USA.

<sup>2</sup> Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany.

<sup>3</sup> Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, 40 Germany.

<sup>4</sup> Department of Biology, University of Maryland, College Park, MD, USA.





<sup>26</sup> Latvian National Museum of Natural History, Riga, Latvia.



- <sup>27</sup> Institute of Biology, University of Latvia, Salaspils, Latvia.
- <sup>28</sup> Latvian Swan Research Society, Kalnciems, Latvia.
- <sup>29</sup> Alaska Department of Fish and Game, Fairbanks, AK, USA.
- <sup>30</sup> National Park Service, Denali National Park and Preserve, Denali Park, AK, USA.
- <sup>31</sup> Science & Technology Branch, Environment & Climate Change Canada, Delta, BC, Canada.
	- <sup>32</sup> Wildfowl & Wetlands Trust, Slimbridge, United Kingdom.
	- <sup>33</sup> Manomet, Inc., Plymouth, MA, USA.
	- <sup>34</sup> Biological Station Rybachy, Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia
- <sup>35</sup> High Arctic Institute, Orion, IL, USA.
	- <sup>36</sup> School of Biological, Earth and Environmental Sciences, University College Cork, Ireland.
	- <sup>37</sup> Alaska Department of Fish and Game, Anchorage, AK, USA.
	- <sup>38</sup> Aquila Environmental, Fairbanks, AK, USA.
	- <sup>39</sup> High Arctic Gull Research Group, Bamfield, BC, Canada.
- <sup>40</sup> Department of Environment and Natural Resources, Government of the Northwest Territories, Inuvik, NT, Canada.
	- <sup>41</sup> Alaska Department of Fish and Game, Palmer, AK, USA.
	- <sup>42</sup> Biodiversity Research Institute, Portland, ME, USA.
	- <sup>43</sup> Reneco International Wildlife Consultants, Abu Dhabi, United Arab Emirates.
- 20 <sup>44</sup> Raptor View Research Institute, Missoula, MT, USA.

<sup>45</sup> Vogeltrekstation-Dutch Centre for Avian Migration and Demography, Wageningen, the Netherlands.

<sup>46</sup> Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands.

- <sup>47</sup> Department of Natural Resource Sciences, McGill University, Ste Anne-de-Bellevue, QC, Canada.
	- <sup>48</sup> Washington Department of Fish and Wildlife, Olympia, WA, USA.





<sup>49</sup> Institute for Avian Research "Vogelwarte Helgoland', Wilhelmshaven, Germany.

<sup>50</sup> Fisheries and Oceans Canada, Winnipeg, MB, Canada.

<sup>51</sup> Great Lakes Institute for Environmental Research, School of the Environment, University of Windsor, Windsor, ON, Canada.

- <sup>52</sup> Littoral Environnement et Sociétés (LIENSs), CNRS, La Rochelle Université, La Rochelle, France.
	- <sup>53</sup> Arctic Raptor Project, Rankin Inlet, NU, Canada.
	- <sup>54</sup> Boise State University, Raptor Research Center, Boise, ID, USA.
	- <sup>55</sup> Research and Technology Centre (FTZ), Kiel University, Büsum, Germany.
- <sup>56</sup> Département de Biologie & Centre d'Études Nordiques, Université Laval, Quebec City, QC, Canada.

<sup>57</sup> Environment & Climate Change Canada, National Wildlife Research Centre, Carleton University, Ottawa, ON, Canada.

- <sup>58</sup> Institute of Geography, Russian Academy of Sciences, Moscow, Russia.
- <sup>59</sup> School of Biology and Ecology, University of Maine, Orono, ME, USA.

 $60$  Centre d'Etudes Biologiques de Chizé, UMR 7372 – CNRS & Université de la Rochelle, Villiers en Bois, France.

<sup>61</sup> Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa.

20 <sup>62</sup> Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington DC, USA.

<sup>63</sup> Northeast Climate Adaptation Science Center, University of Massachusetts Amherst, Amherst, MA, USA.

<sup>64</sup> Department of Integrative Biology, University of Windsor, Windsor, ON, Canada.

<sup>65</sup> 25 Environment & Climate Change Canada, Pacific Wildlife Research Centre, Delta, BC, Canada.

<sup>66</sup> Department of Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, NT, Canada.

<sup>67</sup> US Fish & Wildlife Service, Migratory Bird Management, Anchorage, AK, USA.

<sup>68</sup> National Park Service, Gates of the Arctic National Park & Preserve, Fairbanks, AK, USA.



US Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, ID, USA.

Kidd Biological, Inc., Anacortes, WA, USA.

Institute for Wetlands and Waterbird Research e.V., Verden (Aller), Germany.

Department of Integrative Biology, University of Colorado, Denver, CO, USA.

<sup>73</sup> Polar Knowledge Canada, Cambridge Bay, NU, Canada.

 Department of Environment and Natural Resources, Government of the Northwest Territories, Fort Simpson, NT, Canada.

Manaaki Whenua – Landcare Research, Lincoln, New Zealand.

US Fish & Wildlife Service, Arctic National Wildlife Refuge, Fairbanks, AK, USA.

<sup>77</sup> National Park Service, Alaska Inventory and Monitoring Program, Anchorage, AK, USA.

Korea Institute of Environmental Ecology, Yuseonggu, Daejeon, Republic of Korea.

US Fish & Wildlife Service, Juneau, AK, USA.

Department of Bioscience–Kalø, Aarhus University, Rønde, Denmark.

<sup>82</sup> National Park Service, Lake Clark National Park and Preserve, Anchorage, AK, USA.

<sup>83</sup> Department of Biology and the McCourt School of Public Policy, Georgetown University, Washington, DC, USA.

Wildlife Conservation Society, Arctic Beringia Program, Fairbanks, AK, USA.

University of Manitoba, Winnipeg, MB, Canada.

 Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV, USA.

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA.

 Wageningen Environmental Research, Wageningen University & Research, Wageningen, the Netherlands.

Biology Department, Acadia University, Wolfville, NS, Canada.

<sup>86</sup> Conservation Science Global, Inc. West Cape May, NJ, USA.

Independent researcher, Reykjavik, Iceland.



<sup>91</sup> Laboratory of Ornithology, Institute of Biological Problems of the North FEB RAS, Magadan, Russia.

 $92$  Arctic Research Station of Institute of Plant and Animal Ecology UB, RAS, Labytnangi, Yamal-Nenets Autonomous District, Russia.

<sup>93</sup> 5 Durham University, Durham, United Kingdom.

<sup>94</sup> University of Glasgow, Glasgow, Scotland.

<sup>95</sup> Marine and Environmental Sciences Centre (MARE), Institute of Marine Research (IMAR) and Okeanos R&D Centre, University of the Azores, Horta, Portugal.

- <sup>96</sup> Justus-Liebig University, Gießen, Germany.
- <sup>97</sup> Environment & Climate Change Canada, Yellowknife, NT, Canada.
	- <sup>98</sup> Environment Yukon, Whitehorse, YT, Canada.
	- <sup>99</sup> SOVON, Nijmegen, the Netherlands.
	- <sup>100</sup> US Geological Survey Alaska Science Center, Anchorage, AK, USA.
	- <sup>101</sup> British Columbia Ministry of Environment, Prince George, BC, Canada.
- <sup>102</sup> Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.

<sup>103</sup> US Fish & Wildlife Service, Migratory Bird Management, Denver, CO, USA.

- <sup>104</sup> Center for Conservation Biology, College of William & Mary, Williamsburg, VA, USA.
- <sup>105</sup> HawkWatch International, Salt Lake City, UT, USA.
- <sup>106</sup> H. T. Harvey & Associates, Los Gatos, CA, USA.
- <sup>107</sup> Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark.

<sup>108</sup> Institute of Plant and Animal Ecology, Ural Division Russian Academy of Sciences, Ekaterinburg, Russia.

- <sup>109</sup> National Park Service, Yukon-Charley Rivers National Preserve, Central Alaska Inventory 25 and Monitoring Network, Fairbanks, AK, USA.
	- <sup>110</sup> Hawk Mountain Sanctuary, PA, USA.
	- <sup>111</sup> Wageningen Marine Research, IJmuiden, the Netherlands.
	- <sup>112</sup> Bureau Waardenburg, Culemborg, the Netherlands.

<sup>113</sup> Canadian Wildlife Service, Environment & Climate Change Canada, Saskatoon, SK, Canada.

<sup>114</sup> North Slope Borough, Department of Wildlife Management, Utqiagvik, AK, USA.

<sup>115</sup> School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA.

<sup>116</sup> 5 Earthspan Foundation, Minden, NV, USA.

<sup>117</sup> Ornitela UAB, Vilnius, Lithuania.

\*Correspondence to: Gil Bohrer, bohrer.17@osu.edu

#### 10

**Abstract:** The Arctic is entering a new ecological state, with alarming consequences for humanity. Animal-borne sensors offer a unique window into these changes. Although substantial animal tracking data from the Arctic and Subarctic exist, most are difficult to discover and access. Here we utilize the new Arctic Animal Movement Archive (AAMA), a growing 15 collection of 201 standardized terrestrial and marine animal tracking studies from 1991–present. The AAMA supports public data discovery, preserves fundamental baseline data for the future, and facilitates efficient, collaborative data analysis. With AAMA-based case studies, we document climatic influences on the migration phenology of eagles, geographic differences in adaptive response of caribou reproductive phenology to climate change, and species-specific 20 changes in terrestrial mammal movement rates in response to increasing temperature.

**One Sentence Summary:** The Arctic Animal Movement Archive facilitates long-term and large-scale ecological studies of the Arctic and reveals the timing and extent of changes to animal behavior patterns.

#### 25 **Main Text**

The Arctic and adjacent regions are experiencing the most rapid climate and environmental changes on Earth, caused primarily by anthropogenic greenhouse gas emissions (*1*). Striking trends include warming winter temperatures, ice loss, and earlier spring snowmelt. These changes profoundly affect conditions experienced by animals, including food availability, 30 interspecific competition, predation and increased human disturbances (*2*). Impacts of climate change on Arctic vertebrates include rapid poleward range shifts (*3, 4*), phenological trophic mismatches (*5*), and changes in migration (*6*), foraging, and predator-prey dynamics (*7*). Because rapid environmental change in the Arctic challenges the ability of the region's fauna to adapt, a primary response will likely occur through phenotypic plasticity in the patterns, locations, and 35 timing of their movements (*2*). Documenting and understanding these changes requires multidecadal, pan-Arctic data at multiple trophic levels.

We demonstrate the ecological utility of the Arctic Animal Movement Archive (AAMA), an active, collaborative collection of animal tracking datasets (S.M). Marine ecology archives, such as IOOS-ATN, IMOS, OBIS-SEAMAP, and (*8*), provide insight regarding space use, 40 movement and connectivity (e.g., *9, 10, 11*). Terrestrial animal movement archives are rare and



tend to have a regional or taxonomic focus (e.g., *12*). AAMA is the first Arctic-focused archive with both terrestrial and marine data and is hosted on the global Movebank database. The geographic scope of the AAMA (Fig. 1) includes the Arctic, Arctic-marine, and Subarctic 'boreal forests/taiga' regions defined by (*13*) and (*14*) (S.M.). The dataset contains over 5 15,000,000 occurrences of 8,000 individuals representing 96 species, from 1991–present (Fig. S.1–S.2, Tables S.1–S.4). Combining data from multiple AAMA studies, we show evidence of (1) climate drivers of golden eagle migration phenology, (2) climate adaptation of parturition by caribou, and (3) consequences of increased temperature and precipitation on movements of mammalian predators and herbivores.



15 **Fig. 1. Map of the AAMA boundary and data**. Density of animal locations at logarithmic scale characterizes data availability, not animal density or utilization.





**Fig. 2. Changes in the onset date of golden eagles' summering.** Coefficient estimates (±95% 5 CI) reflecting age-specific changes in response to year, previous winter PDO, sex (reference: females), latitude, the interaction of year and PDO, and age class (reference: juveniles; Tables S.8–S.9). Inset: time series of model-estimated summering.



Behavioral flexibility enables migrants to optimize energy expenditure during migration and adjust arrival at summering grounds (*15, 16*). We used tracking data from 103 individuals during 1993–2017 (S.M., Table S.5) to examine arrival timing to breeding grounds of northward migrating golden eagles ('summering'), modeling it with predictors for age, sex, summering 5 onset latitude, year, and preceding-winter mean Pacific Decadal Oscillation index (PDO).

Mean summering date changed slowly over 25 years (-0.5 days/year). The long-term trend differed among age classes, with adults arriving earliest, followed by sub-adults and then juveniles, and was influenced by winter climate (PDO, Fig. 2; Tables S.8–S.9). Eagles of all age classes began summering later at northern latitudes (1.08 days/degree). The significant 10 interaction of year and previous "warm-phase" PDO explains earlier summering dates for subadults and juveniles, highlighting their known responsiveness to environmental conditions (*16*). These warm-phase winters cause warmer and drier climate with reduced snowpack and an earlier snow-free date. Earlier adult arrival to summering grounds should result from selection and competition for territories, yet local climatic variables affect eagle condition prior to, and energy 15 expenditure during, northward migration (*16*). For sub-adults sampled after 2011, the direct effect of PDO is significant, whereas in the full dataset the direct effect of year replaces PDO (Fig. 2). This period-related difference in inference of climatic drivers highlights the importance of compiling long-term, multi-generational observations. Given the importance of the winter PDO and known impacts of global climate change, golden eagles could face age-specific 20 challenges during migration and at their warming Arctic summering grounds.

The timing of parturition is a key to the demography of wildlife populations, and can be an adaptive response to climate shifts (*17*). For many mammals, the period from late pregnancy through weaning has the highest energetic demands, and thus is timed to occur when vegetation productivity is highest (*18*). Caribou occur in five different ecotypes (Fig. 3) across Boreal and 25 Arctic North America, and are facing global declines (*19*). Using data from 928 individuals during 2000–2017 in northern Canada, we used characteristic patterns of low movement during the calving season to estimate 1647 parturition dates in five populations of barren-ground, boreal, and mountain caribou (S.M., Table S.6).

We found differences in parturition timing and trends among five populations. The 30 southern and northern-boreal populations calved earliest, followed by northern and southern mountain populations (Table S.10). Barren-ground caribou calved later despite occupying a similar latitudinal range as the northern-boreal caribou (Fig. 3). Most importantly, only northern boreal caribou exhibited significant trends towards earlier parturition (0.4–1.1 days/year, Table S.10). This is the first continental-scale retrospective evidence of potential adaptive responses to 35 climate trends by caribou.

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**Fig. 3. Climate-change adaptation of parturition times (PT) of caribou**. Top (map): PT by population. Bottom left: PT trends by population, including five BG subpopulations. Bottom 5 right: PT dates by elevation.



Animals conserve energy by modifying their behavior in response to weather conditions, with important implications for individual fitness and species resilience under climate change (*20*). We tested for effects of temperature and precipitation on seasonal movement rates (m/min) using records from 1,720 individuals of two herbivore and three predator species (black bear, 5 grizzly bear, caribou, moose, and wolf) during 1998–2019 (S.M., Table S.7). We predicted that winter movement rates would decline relative to summer, when energetic costs of selfmaintenance would be highest. Rate would also decline within seasons, during weather conditions that increase the energetic cost of movement (snow that increases energy requirements for movement, higher ambient temperatures during the summer that accelerate 10 metabolism).

All species exhibited lower movement rates during winter relative to summer (Fig. 4). As temperatures increased in summer, wolves and black bears slowed their movement rates, while moose increased their movement rates. In winter, only barren-ground caribou increased movement rates as temperature increased. Snow impeded wolves, boreal caribou, and moose, 15 whereas all species were generally insensitive to summer precipitation. These patterns may reflect asynchronous responses to climate change within and across trophic levels. Climatedriven variation in animal activity is likely to affect species interactions, altering energy expenditure, encounter rates, and foraging success with demographic implications for both predators and prey.

20 As we demonstrate, the AAMA provides a solution to Arctic data collection and sharing challenges. It serves as a critical baseline and resource to identify early signals of local or largescale changes in animal distribution, movement responses, and adaptive traits. Continued shifts in phenology in the Arctic pose challenges to migratory species that encounter changing seasonal fluctuations along migration routes, and at Arctic summering and southern wintering grounds 25 (*21*). Key drivers of population responses, such as migration, parturition, and foraging movement, are undergoing rapid changes, suggesting that climate change is affecting animals in ways that will shape the future of the Arctic.



**Fig. 4. Changes in species-specific movement rates in response to daily maximum**  5 **temperature, summer precipitation and winter snow-water equivalent (SWE).** Odds ratios for continuous covariates represent the positive or negative change in movement rates per one unit change in temperature or precipitation, respectively. Ratios were identified as neutral if credible intervals overlapped one.



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**Supplementary Materials:**

Methods

Figures S.1-S.2

40 Tables S.1-S.10

References (*22-63*)



5



## Supplementary Materials for

### **Ecological insights from three decades of animal movement tracking across a changing Arctic**

**Authors:** Sarah C. Davidson, Gil Bohrer\* , Eliezer Gurarie, Scott LaPoint, Peter J. Mahoney, Natalie T. Boelman, Jan U.H. Eitel, Laura R. Prugh, Lee A. Vierling, Jyoti Jennewein, Emma Grier, Ophélie Couriot, Allicia P. Kelly, 10 Arjan J.H. Meddens, Ruth Y. Oliver, Roland Kays, Martin Wikelski, Tomas Aarvak, Joshua T. Ackerman, José A. Alves, Erin Bayne, Bryan Bedrosian, Jerrold L. Belant, Andrew M. Berdahl, Alicia M. Berlin, Dominique Berteaux, Joël Bêty, Dmitrijs Boiko, Travis L. Booms, Bridget L. Borg, Stan Boutin, W. Sean Boyd, Kane Brides, Stephen Brown, Victor N. Bulyuk, Kurt K. Burnham, David Cabot, Michael Casazza, Katherine Christie, Erica H. Craig, Shanti E. Davis, Tracy Davison, Dominic Demma, Christopher R. DeSorbo, Andrew Dixon, Robert Domenech, 15 Götz Eichhorn, Kyle Elliott, Joseph R. Evenson, Klaus-Michael Exo, Steven H. Ferguson, Wolfgang Fiedler, Aaron Fisk, Jérôme Fort, Alastair Franke, Mark R. Fuller, Stefan Garthe, Gilles Gauthier, Grant Gilchrist, Petr Glazov, Carrie E. Gray, David Grémillet, Larry Griffin, Mike Hallworth, Autumn-Lynn Harrison, Holly L. Hennin, J. Mark Hipfner, James Hodson, James A. Johnson, Kyle Joly, Kimberly Jones, Todd E. Katzner, Jeff W. Kidd, Elly C. Knight, Michael N. Kochert, Andrea Kölzsch, Helmut Kruckenberg, Benjamin J. Lagassé, Sandra Lai, Jean-20 François Lamarre, Richard B. Lanctot, Nicholas C. Larter, A. David M. Latham, Christopher J. Latty, James P. Lawler, Don-Jean Léandri-Breton, Hansoo Lee, Stephen B. Lewis, Oliver P. Love, Jesper Madsen, Mark Maftei, Mark L. Mallory, Buck Mangipane, Mikhail Y. Markovets, Peter P. Marra, Rebecca McGuire, Carol L. McIntyre, Emily A. McKinnon, Tricia A. Miller, Sander Moonen, Tong Mu, Gerhard J.D.M. Müskens, Janet Ng, Kerry L. Nicholson, Ingar Jostein Øien, Cory Overton, Patricia A. Owen, Allison Patterson, Aevar Petersen, Ivan Pokrovsky, 25 Luke L. Powell, Rui Prieto, Petra Quillfeldt, Jennie Rausch, Kelsey Russell, Sarah T. Saalfeld, Hans Schekkerman, Joel A. Schmutz, Philipp Schwemmer, Dale R. Seip, Adam Shreading, Mónica A. Silva, Bryan W. Smith, Fletcher Smith, Jeff P. Smith, Katherine R.S. Snell, Aleksandr Sokolov, Vasiliy Sokolov, Diana V Solovyeva, Mathew S. Sorum, Grigori Tertitski, J.F. Therrien, Kasper Thorup, T. Lee Tibbitts, Ingrid Tulp, Brian D. Uher-Koch, Rob S.A. van Bemmelen, Steven Van Wilgenburg, Andrew L. Von Duyke, Jesse L. Watson, Bryan D. Watts, Judy A. 30 Williams, Matthew T. Wilson, Jay Wright, Michael A. Yates, David J. Yurkowski, Ramūnas Žydelis, Mark Hebblewhite

Correspondence to: bohrer.17@osu.edu

#### **This PDF file includes**

35 Materials and Methods Figs. S.1 to S.2 Tables S.1 to S.10

#### 40 **Materials and Methods:**

#### Arctic Animal Movement Archive (AAMA)

The AAMA enables the discovery and use of Arctic and Subarctic animal movement data. The AAMA is hosted on Movebank (movebank.org), a global research platform for animal tracking and bio-logging data. We defined the geographic scope of the AAMA to include marine and terrestrial Arctic areas defined by the Arctic Monitoring and



Assessment Programme *(13)* (shapefile available from https://www.amap.no/about/geographical-coverage) and Subarctic land regions represented as 'boreal forests/taiga' as classified by the Nature Conservancy *(14)* (shapefile available from http://maps.tnc.org/files/metadata/TerrEcos.xml). The AAMA boundary and the observation density within it are shown in Fig. 1. We calculated the density of animal occurrences shown in Fig. 1 as location counts 5 within 10-km hexagonal grid cells (spacing 9.68 km, area 95.98 km<sup>2</sup>) in equal area projection in R using the *dggridR* package (*22*).

The AAMA is a living archive. Many ongoing studies continuously add data, and new participants and studies can join. Data in the AAMA are organized into studies, with each study (i.e. dataset) managed by one or more data owners. Studies participating in the AAMA as of November 2019 are listed in Table S.1. Participating 10 studies include data within the geographic area described above and can include additional data from other regions, thus supporting inclusion of species that spend substantial portions of their annual life cycle in temperate or tropical regions, and future inclusion of species that enter the region due to northward range shifts. The AAMA preserves the data, harmonizes it, and makes it discoverable by publishing the metadata. All data are curated to ensure they are accurately stored and include sufficient descriptive detail. AAMA Participants retain ownership of their data, with 15 the option to allow public download or limit access to approved users. Study-level information including species, tagging method, number of animals and locations, time period covered, project description and available citations, and owner contact information are publicly available, searchable online, and by API. In all cases, data owners can be contacted directly to discuss data access and proposed uses. Location and other sensor data from the majority of participating studies are available for public download from the AAMA (currently 56% of the data), and many 20 represent datasets formally published through the Movebank Data Repository. The AAMA offers assistance for potential users in negotiating data sharing and maintains current contact information for study owners. Reasons for access-controlled sharing include (i) data are still being actively collected and are not yet quality controlled, (ii) public knowledge of animal locations could compromise conservation efforts, and (iii) legal or contractual restrictions prohibit uncontrolled public data access. The AAMA's support for public and controlled-access sharing 25 provides a solution that preserves and allows collaboration using data that would otherwise remain undiscoverable, and in many cases would eventually be lost (e.g., after the data owner retires). All data in the AAMA were collected using appropriate animal care permissions (Table S.3). Funding sources for data collection are provided in Table S.4. Current information about participating studies, how to download or request data, and how to join the archive and provide new datasets is available at the AAMA landing page (https://www.movebank.org/cms/movebank-30 content/arctic-animal-movement-archive).

The organization of studies in the AAMA on the Movebank platform represents significant efforts to document and organize data using a consistent format, vocabulary, and set of quality-control procedures. This reduces the time needed to prepare data for sharing and integration in combined analyses, and provides a single access point, thus minimizing logistical efforts needed for construction of data ensembles to address large-scope 35 research questions in meaningful meta-analyses. Furthermore, automated data feeds and management tools promote further participation by allowing data owners to efficiently add and maintain studies over time. We solicit additional participation in the AAMA, both by data owners and those conducting new analyses. As the archive and period of record grow, it will allow increasingly rigorous testing of hypotheses about human-driven, climate-induced, or other natural effects on animal movement, distribution and behavior.

#### 40 Case Study 1. Long-term data reveal influence of decadal climate patterns on summering behavior in a migratory raptor We used 569,720 location estimates collected from 146 golden eagles (*Aquila chrysaetos*) in 12 AAMA studies across western North America (Table S.5). Records were imported into R via the *move* package (*23*). We assigned all individuals to one of three age categories: juvenile (survived up to the onset of its  $2<sup>nd</sup>$  southbound migration), sub-adult (surviving up to the onset of its  $4<sup>th</sup>$  southbound migration), or adult (surviving past the onset of its  $4<sup>th</sup>$ southbound migration) (*16, 24*). We incorporated into analyses instances where individuals were observed during an age-class transition. Breeding status was not considered in analyses because it was not determined for all individuals. We identified the onset of golden eagle summering behavior via a mechanistic range shift analysis (MRSA (*25*)) in R with the *marcher* package (*26*). The model was fit with the maximum likelihood method, and we 50 used the Ornstein-Uhlenbeck model option to estimate ranging behavior. We modified the MRSA slightly by

forcing the model to fail if a data gap of >30 days occurred. We inspected start dates and locations to remove



spurious model results due to tag deployments that ended during spring migration or began during summer. This process yielded 179 summering onset estimates with modelled start and end dates made by 103 eagles (Table S.5).

We used linear mixed-effects models in R via the *lme4* package (version 1.1-17) (*27*), fit by restricted maximum likelihood to assess the significance of year (fixed, continuous, scaled), eagle sex and age during 5 migration (both fixed, categorical), latitude (fixed, continuous), and PDO (fixed, continuous) in explaining golden eagle summering onset date. For adults and subadults, we included eagle individuals as a random term to account for repeated measures for some individuals ( $n = 49$ ), but not for juveniles, due to a lack of repeated measures. We meancentered year and included an interaction between year and PDO. We averaged the monthly mean PDO (*28, 29*) of the preceding winter (November to March) to explore the influence of this large-scale climate indicator on golden 10 eagle behavioral phenology. Multi-collinearity between predictor variables did not exceed recommended varianceinflation levels (*30*). We performed model selection in R using the *dredge* function of the *MuMIn* package (*31*) and report results from the conditional averaged models. We first ran a model including eagles of all age classes to explore differences in age classes. We then analyzed each age class separately to facilitate interpretation. Because few summering onsets before 2011 were available for adults and sub-adults, we also compared model-averaged 15 results for the full sets of adult and subadult observations  $(n = 89, n = 72,$  respectively) to those for the post-2011 adult and subadult observations ( $n = 83$ ,  $n = 67$ , respectively).

#### Case Study 2. Large-scale geographic differences in parturition timing of caribou

We used caribou movement data in 13 AAMA studies (Table S.6). Among the caribou in our study, woodland caribou (*Rangifer tarandus caribou*) are considered a separate subspecies from barren-ground caribou (*R. t.*  20 *groenlandicus*), which are known for their long-distance calving migrations. Woodland caribou are further classified as belonging to different ecotypes, including boreal and mountain, which differ by habitat and behavioral phenotype. Following exploratory analysis, we further partitioned woodland caribou by geographic area into northern and southern mountain and boreal caribou. Barren-ground caribou data were partitioned into their largely coherent reproductive subpopulations (herds).

25 Parturition dates were estimated by adapting methods described in (*32*) for each of the two subspecies. For *R. t. caribou*, we analyzed movements between April 28 and June 30 and found times when movement activity decreased suddenly and persistently below 5 threshold speeds (10, 15, 20, 25, and 30 m/h), and conservatively retained those parturitions where three of five thresholds agreed within a day of each other. For barren-ground caribou, which calve significantly later and shortly after completing a long-distance migration, we adapted the 30 individual-based method (*32*), which fits a non-calving model, in which movement rates remain constant throughout the study period, and a calving model, where there is a sudden drop in movement rate followed by a progressive increase. The models were fit using maximum likelihood, and AIC was used as a criterion to determine which model was selected. Tests for the effects of latitude, longitude, elevation, and year on parturition dates were conducted using a combination of linear models, generalized additive models, and mixed effects models, with individuals as a 35 random effect. The *R. t. groenlandicus* (barren-ground) population is subdivided into five subpopulations (herds), which were also modeled as a random effect. Results are summarized in Table S.10.

Case Study 3: Temperature and precipitation response in movement rates of terrestrial mammals We compiled movement paths for 1,720 individuals representing five mammalian species from 22 AAMA studies: black bear, *Ursus americanus*; grizzly bear, *U. arctos*; caribou, *R. tarandus ssp.*; moose, *Alces alces*; and 40 wolf, *Canis lupus* (Table S.7). We calculated step lengths (m) and location sampling interval (min) along each movement time series, excluding locations with sampling intervals longer than 24 hours. We annotated movement data with daily maximum temperatures (°C) and summertime precipitation or winter snow water equivalent (SWE) estimates using the Daymet data product (*33*). To match the temporal scale of Daymet, we aggregated movements by estimating daily mean step lengths and sampling intervals for each day within an individual's time series. In 45 order to reduce the influence of seasonally dependent behaviors (e.g., migration or parturition), we partitioned data into January-only (peak winter) and July-only (peak summer) datasets. As in case study 2, we treated the two subspecies of caribou (*R. t. groenlandicus* and *R. t. caribou*) as distinct groups within our analysis due to anticipated differences in daily movement rates. We also excluded bears from the winter analyses due to lack of data; however, the very nature of their hibernation represents a reduced overwinter movement rate..



We assessed the influence of daily maximum temperature and cumulative precipitation on daily movement rates (m•min<sup>-1</sup>) using a generalized linear mixed model (GLMM) framework with the *lme4* R package (27). Because movement rates are positive continuous, we used discretized step lengths (rounded to the nearest meter) as the response and location sampling interval as an offset in a GLMM with negative binomial errors. Prior to modeling, 5 we standardized daily temperature and precipitation estimates by subtracting means and dividing by one standard deviation, each estimated at the study level by season in an effort to account for regional differences in exposure to weather conditions. We evaluated two models for each species represented by an interaction between season (January or July) and a single climate metric: season × temperature and season × precipitation. However, we used SWE ( $kg \cdot m^2$ ) as a measure of snow cover during the winter and daily total precipitation (mm) during the summer. 10 We included random intercepts for individual nested within study crossed within year to account for variation in individual movement rates and sample sizes within and across studies. As there was a single study for bears, we included random intercepts for individual and year only. Variable effectiveness was determined by coefficient confidence interval overlap with zero, where an overlap indicating the effect is neutral (i.e., no change).



## **Fig. S1.**

**Summary of the content of studies participating in the AAMA as of November 2019.** Temporal range and number of individuals in each study (Table S.1) colored by species group (Table S.2). Note logarithmic scale on y-5 axis.





1991 1993 1995 1997 1999 2001 2003 2005 2007 2009 2011 2013 2015 2017 2019



### **Figure S.2.**

**The number of locations per year per species group for data participating the AAMA as of November 2019**. The number of locations includes only those with locations within the AAMA boundary. See Table S.2 for species assigned to each species group.





#### **Table S1.**

Studies participating in the AAMA as of November 2019. 'Study name' and 'Study ID' refer to the dataset as stored in a study on Movebank. 'Species' and 'Years' are based on locations within the AAMA boundary. 'Animals' shows the number of individuals with locations within 5 the AAMA boundary, followed in parentheses, by the total number of animal individuals that were tracked in the study, regardless of location. Superscript 'CSx' in 'Study name' indicates studies used in the case studies where x is the case study number (Tables S.5–S.7). 'Data ref' lists the citation for published study datasets. Current information about participating studies, and information about how to join, is available at the AAMA landing page.





































### **Table S2.**

Species-level and species group summary of data from studies participating in the AAMA as of November 2019.









### **Table S.3.**

Permits, licenses and approved protocols for research, animal handling and tagging related to studies participating in the AAMA as of November 2019. ACC = Animal Care Committee, ACUC = Animal Care and Use Committee, AWC = Animal Welfare Committee, IACUC = Institutional Animal Care and Use Committee, WCC = Wildlife 5 Care Committee.





### 2018-001



![](_page_37_Picture_233.jpeg)

![](_page_38_Picture_0.jpeg)

![](_page_38_Picture_211.jpeg)

![](_page_39_Picture_232.jpeg)

![](_page_40_Picture_237.jpeg)

![](_page_41_Picture_0.jpeg)

![](_page_41_Picture_215.jpeg)

![](_page_42_Picture_0.jpeg)

![](_page_42_Picture_185.jpeg)

![](_page_43_Picture_0.jpeg)

![](_page_43_Picture_207.jpeg)

![](_page_44_Picture_1.jpeg)

![](_page_44_Picture_232.jpeg)

![](_page_45_Picture_231.jpeg)

![](_page_46_Picture_0.jpeg)

![](_page_46_Picture_1.jpeg)

### **Table S.4.**

Acknowledgements and funding for studies participating in the AAMA. Organization funding might extend beyond the subdivisions, grants, and programs listed.

![](_page_46_Picture_152.jpeg)

![](_page_47_Picture_1.jpeg)

![](_page_47_Picture_145.jpeg)

![](_page_48_Picture_1.jpeg)

![](_page_48_Picture_165.jpeg)

![](_page_49_Picture_151.jpeg)

![](_page_50_Picture_0.jpeg)

![](_page_50_Picture_150.jpeg)

![](_page_51_Picture_1.jpeg)

![](_page_51_Picture_147.jpeg)

![](_page_52_Picture_1.jpeg)

![](_page_52_Picture_169.jpeg)

![](_page_53_Picture_1.jpeg)

![](_page_53_Picture_170.jpeg)

![](_page_54_Picture_0.jpeg)

### **Table S.5.**

Studies used in Case Study 1, 'long-term data reveal importance of decadal climate patterns on summering behavior in a migratory raptor'.

![](_page_54_Picture_172.jpeg)

![](_page_55_Picture_0.jpeg)

## **Table S.6.**

Studies used in Case Study 2, 'large-scale geographic differences in parturition timing of caribou'.

![](_page_55_Picture_185.jpeg)

![](_page_56_Picture_0.jpeg)

## **Table S.7.**

Studies used in Case Study 3, 'temperature and precipitation response in movement rates of terrestrial mammals'.

![](_page_56_Picture_336.jpeg)

#### **Table S.8.**

Mixed-model results from Case Study 1, 'long-term data reveal importance of decadal climate patterns on summering behavior in a migratory raptor'. Conditional average linear mixed-model results for golden eagle summering onset dates from 1993 to 2017. Only models in which the parameter of interest is retained within the 5 model are used in the averaging. We scaled year by centering on the mean and dividing by the standard deviation. Here we list the covariates, coefficient estimates from model averaging ('estimate'), standard errors ('se'), Satterthwaite degrees of freedom ('df'), z-values, and p-values ('Pr(>|z|)'). The full model did not have the highest weight for juveniles or sub-adults  $> 2011$ , but we report it here for consistency with other age class models.

![](_page_57_Picture_403.jpeg)

![](_page_58_Picture_1.jpeg)

![](_page_58_Picture_124.jpeg)

![](_page_58_Picture_125.jpeg)

### **Table S.9.**

Model selection results (weight > 0.01) from Case Study 1, 'long-term data reveal importance of decadal climate patterns on summering behavior in a migratory raptor', evaluating the influence of year (fixed, continuous, centered and scaled), latitude of summering behavior start (fixed, continuous), eagle sex (fixed, categorical; excluded in 5 'Juvenile' model), eagle age (fixed, categorical; only included in 'All' model), mean monthly PDO index for the proceeding winter (PDO; fixed, continuous), and the interaction of year and PDO. We included individual identifier as a random term and fit our linear mixed-effect model by restricted maximum likelihood. Here we present a subset of the models, ranked by model weight, including their degrees of freedom (df), log-likelihood (LL), pseudo-R<sup>2</sup> (Nagelkerke's modified statistic; R<sup>2</sup>), Bayesian Information Criterion (BIC), Akaike Information Criterion corrected 10 for small sample sizes (AICc), and delta AICc (delta).

![](_page_59_Picture_541.jpeg)

![](_page_60_Picture_352.jpeg)

![](_page_61_Picture_0.jpeg)

#### **Table S.10**

Population-level summary statistics for caribou parturition analysis (case study 2). The trend for mountain caribou was modeled by generalized additive models (GAMs) that include linear latitude and longitude effects and a spline on elevation. The woodland caribou trend models only include latitude and longitude effects. The barren-ground 5 trend model is a linear mixed effects models with random intercepts and slopes (year effect) on herd (subpopulation) as a random effect. The  $r^2$  values are the *conditional* as opposed to *marginal*  $r^2$  following (63). The *p*value and trend are on the collective main effect and do not account for variation among herds.

![](_page_61_Picture_270.jpeg)