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1 Landfast ice: a major driver of reproductive success in a polar seabird

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3 Biology Letters

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18

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21

22 **Keywords**

23 Emperor penguin; sea ice; breeding success; climate window analysis; non-linear effect

24 **Abstract**

25

26 In a fast-changing world, polar ecosystems are threatened by climate variability. Understanding the roles of
27 fine-scale processes, linear and non-linear effects of climate factors on the demography of polar species is
28 crucial for anticipating the future state of these fragile ecosystems. While the effects of sea ice on polar marine
29 top predators are increasingly being studied, little is known about the impacts of landfast ice on this species
30 community. Based on a unique 39-year time-series of satellite imagery, *in situ* meteorological conditions and
31 on the world's longest dataset of emperor penguin *Aptenodytes forsteri* breeding parameters, we studied the
32 effects of fine-scale variability of landfast ice and weather conditions on this species reproductive success. We
33 found that longer distances to the landfast ice edge (i.e. foraging areas) negatively affected the overall
34 breeding success but also the fledging success. Climate window analyses suggested that chick mortality was
35 particularly sensitive to landfast ice variability between August and November. Snowfall in May also affected
36 hatching success. Given the sensitivity of landfast ice to storms and changes in wind direction, important future
37 repercussions on the breeding habitat of emperor penguins are to be expected in the context of climate
38 change.

39

40 1. Introduction

41

42 Polar ecosystems are subject to local and regionally contrasted sea ice trends due to climate change
43 [1,2]. Given the complexity of these trends, which are tightly linked to the atmosphere and the ocean
44 dynamics, there is an urgent need to measure and forecast how polar marine populations will respond to sea
45 ice habitat changes [3,4]. Among the studies that have investigated the impacts of climate change and
46 variability on population dynamics in the Southern Ocean [5,6], a thorough understanding of the fine-scale
47 processes by which climate affects the population dynamics of polar organisms is still lacking, thereby
48 preventing the scientific community from improving model projections to correctly assess the future states of
49 polar populations and ecosystems. Given that population dynamics are driven by several demographic
50 components whose sensitivities to climatic factors vary [7,8], it is important to investigate the links between
51 climate and each demographic component. Determining the spatial and temporal scales at which climate
52 variability affects biological parameters is also of prime importance [9]. Also crucial for improving projections,
53 long-term multi-decadal biological series are required to detect non-linear effects of climate on populations
54 [10–13]. The obtention of such long time-series is however often limited by logistical challenges associated
55 with conducting long-term studies in these remote and extreme areas.

56 Many Antarctic marine top predators, such as seals and seabirds, are intricately linked to landfast ice (LFI),
57 i.e. the narrow band of coastal, compact sea ice held in place by ice shelves and grounded icebergs [14],
58 throughout their breeding period [15–17]. Therefore, LFI variability, such as extreme extent or early break up,
59 can profoundly impact their breeding areas and breeding success [19,20]. However, functional relationships
60 between LFI variability and demographic parameters of polar marine predators remain poorly known due to
61 the scarcity of biological datasets and the difficulty to characterize LFI variability over long time periods.

62 To improve our understanding of how polar species will respond to future climate changes, we explored
63 the role LFI variability and *in situ* meteorological conditions have on the overall breeding success, but also the
64 fledging and hatching success of a unique sea ice sentinel species [20], the emperor penguin (*Aptenodytes*
65 *forsteri*). We used the longest historical time-series of Antarctic LFI collected by the Advanced Very High

66 Resolution Radiometer (AVHRR) and the Moderate-Resolution Imaging Spectroradiometer (MODIS), covering
67 the years 1979 to 2017, i.e. since the inception of modern satellite monitoring. We also used the world's
68 longest time-series of emperor penguin breeding parameters, collected at Pointe Géologie, Adélie Land, since
69 1952. The novelty of this research, while relying on previous studies (e.g. [21–26]), lies in i) assessing the
70 climate effect on different components of the reproduction, ii) using the longest time-series available for LFI
71 and emperor penguin reproduction, iii) taking into account the relative contribution of fine-scale processes
72 (local LFI and *in situ* meteorological conditions), iv) exploring different time windows of these effects, and v)
73 testing non-linear effects.

74

75 **2. Material and methods**

76

77 (a) Landfast ice data

78 Three sources of satellite imagery were used to cover the 1979–2017 period and aggregate LFI data (electronic
79 supplementary material; see figure S1 for examples):

80 1) 1979–1991: visible (when available) or thermal infrared images from AVHRR's Global Area Coverage

81 (GAC) mode (spatial resolution of 4 kilometres per pixel; km/px).

82 2) 1992–1999: visible (when available) or thermal infrared images from the AVHRR Coastal Atlas of East

83 Antarctica [27] (resolution of 1.1 km/px).

84 3) 2000–2017: LFI maps from Moderate-Resolution Imaging Spectroradiometer (MODIS) images

85 (resolution of 1 km), classified by Ref. [28].

86 Distances between the penguin colony location and the nearest landfast ice edge (LFIE) (i.e., proxy for access

87 to the ocean) and landfast ice areas (LFIA) were extracted from the images.

88

89 (b) Meteorological data

90 Meteorological data were obtained from the French weather station of Dumont D'Urville. Three

91 parameters were used in this study: the number of days per month with i) temperatures under -10°C , ii) winds

92 above 28 m/s, and iii) snowfall. We hypothesised that egg loss during incubation and chick mortality could be
93 enhanced during cold and windy conditions caused by katabatic winds and winter storms [15]. Heat loss due
94 to cold temperatures and strong winds, which could be enhanced by snowfall, may increase chick mortality.

95

96 (c) Reproductive data

97 Data are similar to those used by Refs. [21,29] with updated estimates (electronic supplementary
98 material). From count data we estimated 'breeding success' as the number of fledged chicks divided by the
99 number of breeding pairs; 'hatching success' as the number of breeding pairs minus the number of dead eggs
100 divided by the number of breeding pairs; and 'fledging success' as the number of fledged chicks divided by the
101 number of breeding pairs minus the number of dead eggs. Breeding success was estimated over the period
102 1979–2017; hatching and fledging success over the period 1983–2017.

103

104 (d) Climate window analysis

105 We performed a 'climate window analysis' using the R package *climwin*, following the steps described in Ref.
106 [30]. Climate window analyses determine, without any *a priori* hypothesis, the best climate window(s) (i.e.
107 candidate models) that identify potential climate signals between biological and climate data. Two datasets
108 were analysed: one that contained our monthly climate data, i.e. landfast ice or meteorological data covering
109 the 1979–2017 period, and one that contained information on the response variable, i.e. breeding, hatching,
110 and fledging success. For each climate window, a model was computed. Akaike Information Criteria (AICs)
111 were used for ranking and comparing different candidate climate windows, and then for assessing the best
112 models, their uncertainty, explanatory power, and applicability. Details on the analysis and outputs of the
113 analysis are provided in the electronic supplementary material. The full dataset and codes can be found on
114 Dryad [31].

115

116 **3. Results**

117

118 (a) Reproduction time-series

119 Hatching success was the most stable reproductive parameter (mean \pm SD = 0.82 ± 0.07 , CV = 8.3 %), while
120 fledging success (0.65 ± 0.30) and breeding success (0.53 ± 0.25) were more variable (CV = 46.4 % and 46.5 %,
121 respectively; figure 1a). Hatching success increased during the study period (slope = 0.051 ± 0.007 (SE), $p <$
122 0.001), while fledging success (slope = -0.003 ± 0.052 , $p = 0.96$) and breeding success (0.026 ± 0.040 , $p = 0.52$)
123 remained stable (figure 1a). Variations in both fledging and breeding successes seemed to co-vary with the
124 LFIA, but even more so with the distance to the nearest LFIE (figure 1b-c).

125

126 (b) Climate window analysis

127 Breeding success was higher for shorter distances to the LFIE between August and November ($p_{\text{randomization}}$
128 = 0.006 ; adjusted $R^2 = 0.4$), while the LFIA did not have a significant influence (i.e. based on the randomization
129 test; table 1, figure 2a). The number of days per month with temperatures under -10°C , with winds above 28
130 m/s, and with snowfall did not influence the breeding success (table 1). Neither the LFIA nor the number of
131 days per month with winds above 28 m/s or temperature below -10°C had an influence on the hatching
132 success (table 1). However, the hatching success appeared to be influenced by the number of days with
133 snowfall in May ($p_{\text{randomization}} = 0.0003$, adjusted $R^2 = 0.3$; table 1, figure 2c). This relationship was non-linear,
134 with hatching success increasing with the proportion of days with snowfall per month up to 37% and remaining
135 stable or decreasing slightly for higher proportions. Finally, fledging success was higher for shorter distances
136 to the LFIE in November ($p_{\text{randomization}} = 0.035$, adjusted $R^2 = 0.5$; table 1, figure 2b), while the LFIA, the number
137 of days per month with temperature below -10°C , with winds above 28 m/s, and with snowfall did not have a
138 significant influence (table 1). Fledging success declined non-linearly with the nearest distance to the LFIE,
139 with an accelerated decline for distances greater than ca. 50 km.

140

141 **4. Discussion**

142 We showed that, over 39 years, different components of the reproduction of an Antarctic seabird were
143 affected by fine-scale LFI and *in situ* meteorological conditions at different times of its breeding season, and,
144 importantly, these relationships were non-linear.

145 Adult emperor penguins during the breeding season forage and hunt by diving at the edge of the LFI
146 in cracks, flaw leads, and polynyas [32]. Longer distances between the colony and foraging grounds accessed
147 by the LFIE imply lower chick-feeding frequency, and thus lower chick growth with negative consequences on
148 fledging and breeding success. Using historical AVHRR and recent MODIS images, our study brings important
149 and novel results. First, we identified that distance to nearest LFIE particularly affected fledging success in
150 November (and the second-best model identified a window between August and November), indicating that
151 chick mortality was the main cause of declining breeding success with increasing distance to LFIE. Second, this
152 relationship was nonlinear, with over 50% chick mortality when the distance to LFIE exceeded ca. 65 km. Non
153 linearity could be detected by extending the time series from 8 years in a previous work [26] to nearly 40 years
154 in our study. Third, we identified that the best climate window explaining the relationships between distance
155 to LFIE (i.e. foraging grounds) and breeding success was between August and November, suggesting chicks
156 were particularly sensitive to environmental variability during this period of high energetic demands for body
157 growth [33,34].

158 Reproduction has been monitored at extremely few other emperor penguin colonies. Surprisingly, no
159 relationship was found between LFI and breeding success of emperor penguins at Taylor Glacier colony [35].
160 Although this may depict the complex interactions between environment and penguin foraging behaviour and
161 their consequences for breeding performances, ref. [35] used distance to LFIE in April and September, and our
162 time windows analysis indicated that these months did not represent the full critical period for fledging and
163 breeding success. Nevertheless, this highlights the need to monitor multiple sites in order to understand how
164 sea ice variability, and especially LFI, is affecting the global emperor penguin population.

165 Our study supports previous findings that it is crucial to consider both fine-scale climate processes and
166 fine-scale temporal windows when investigating the relationships between climate variability and
167 demographic traits [9,36]. Despite the diversity of studies that have investigated the effect of climate change

168 on polar species, there is a strong need to account for the factors that control population dynamics at
169 local/regional scales in order to understand how they may modulate the effects of large-scale environmental
170 variations on long-term population trend [13]. For example, ref. [37] compared the influence of environmental
171 factors on the breeding success of snow petrels (*Pagodroma nivea*) at Casey station with the colony of Adélie
172 Land, and showed that despite similarities in the biological processes controlling snow petrel breeding success,
173 the correlation of large-scale environmental factors with breeding success differed substantially between the
174 two colonies, likely due to the effects of the environmental factors at the local/regional scale.

175 Landfast ice variability may have important indirect effects that we did not consider in this study. For
176 example, LFI break-ups could contribute to the phytoplankton seeding process (e.g. [38–40]) and may drive a
177 phytoplankton bloom associated with trophic cascades. This could in turn benefit emperor penguins through
178 bottom-up processes with a temporal lag depending on the timing within the breeding period. In the Arctic,
179 longer temporal lags between sea ice melting and phytoplankton bloom resulted in rapidly decreasing
180 breeding performance for little auks (*Alle alle*) and Brünnich’s guillemots (*Uria lomvia*) [41]. Thus, considering
181 local to regional-scale phenology in the development of potential phytoplankton blooms in responses to LFI
182 variability may help understand climate-driven environmental impacts on seabirds.

183 During breeding, individual emperor penguins do not use a fixed nest site as do other penguins.
184 Therefore, the colony is mobile during the breeding season and can move several hundred meters or even a
185 few kilometers. Therefore, the selection of nest site (and experience to nest site) is not relevant for this
186 species. However, there might be selection for sites where colonies are situated, as these sites are generally
187 occupied for long time periods (several decades at least), as our results suggest a strong selection pressure
188 from environmental factors such as LFIE. Nevertheless, the environmental factors affecting colony site
189 selection have not been investigated and quantified to date.

190 Finally, none of the meteorological variables, except snow falls for the hatching success, had an
191 influence on reproductive parameters. The positive relationship between the number of days with snowfall in
192 May and the hatching success may be associated with the hydration of males during their long fasting period
193 of ca. four months. We speculate that important snowfalls in May allow males to supplement their water

194 intake by eating snow, thus decreasing dehydration potentially leading to the abandonment of the egg before
195 it hatches. Indeed, field observations during winter indicate that male emperor penguins eat snow all along
196 the incubation period ([42]; CB, pers. obs.).

197 Our results bring new insights on the proximate mechanisms through which a poorly known polar
198 habitat feature, LFI, affects demographic parameters of polar top predators. We note that, although we might
199 be able to better predict the future state of polar populations once such fine-scale processes are fully
200 understood, population projections based on sea ice models (e.g. [43]) remain hampered by the fact that these
201 models project sea ice extent but do not provide information on LFI dynamics yet. Important future
202 repercussions on the breeding habitat of emperor penguins and ultimately their persistence are to be
203 expected in the context of climate change [2] given the sensitivity of LFI to storms and changes in wind
204 direction [44], as well as the recently observed strong and opposed LFI trends in adjacent regions [45]. Given
205 the demographic sensitivity of emperor penguins associated with postglacial warming leading to a major
206 southward expansion [46], major shifts such as decline or extinction of emperor penguin populations are
207 expected under anthropogenic climate change.

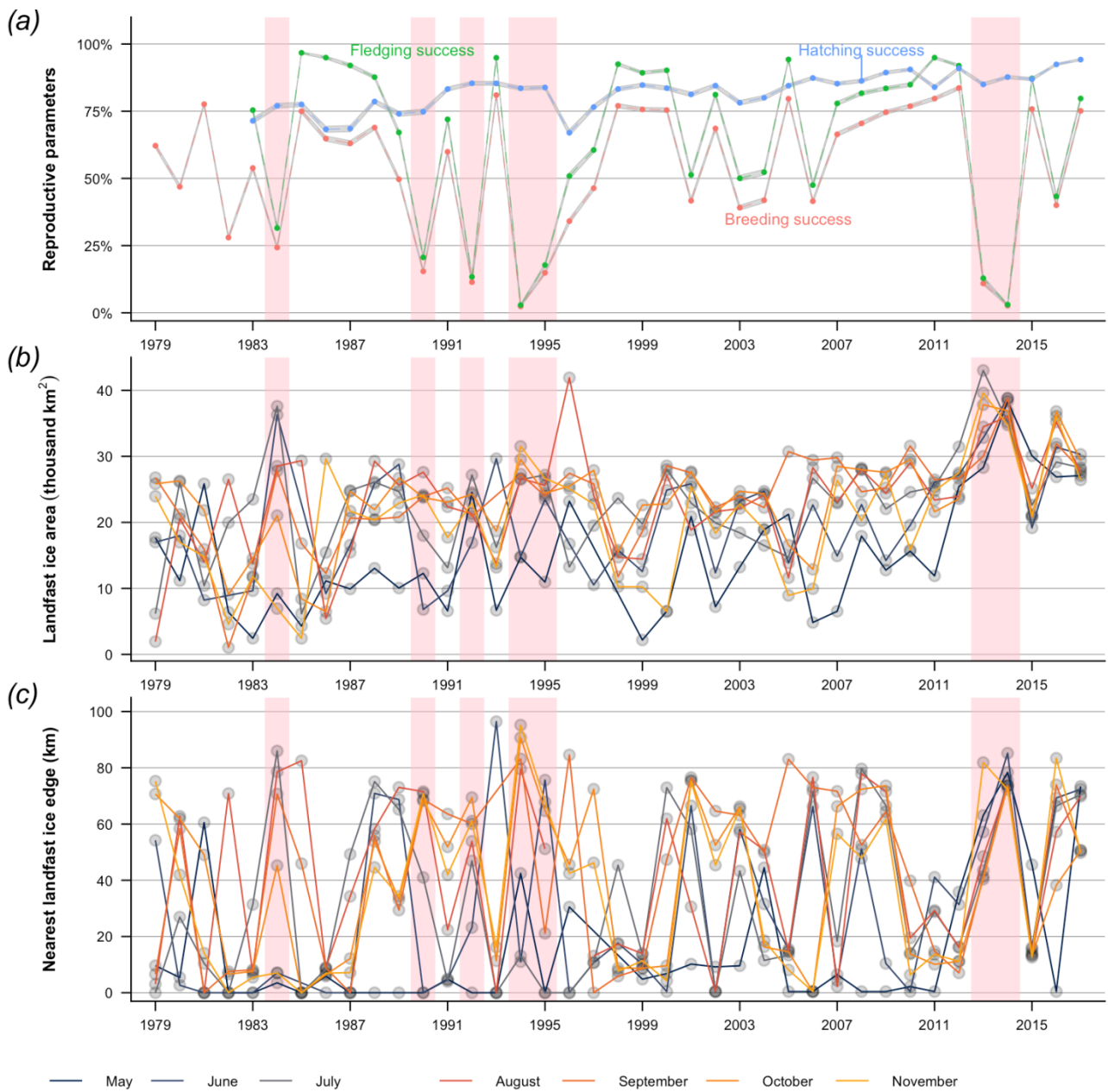
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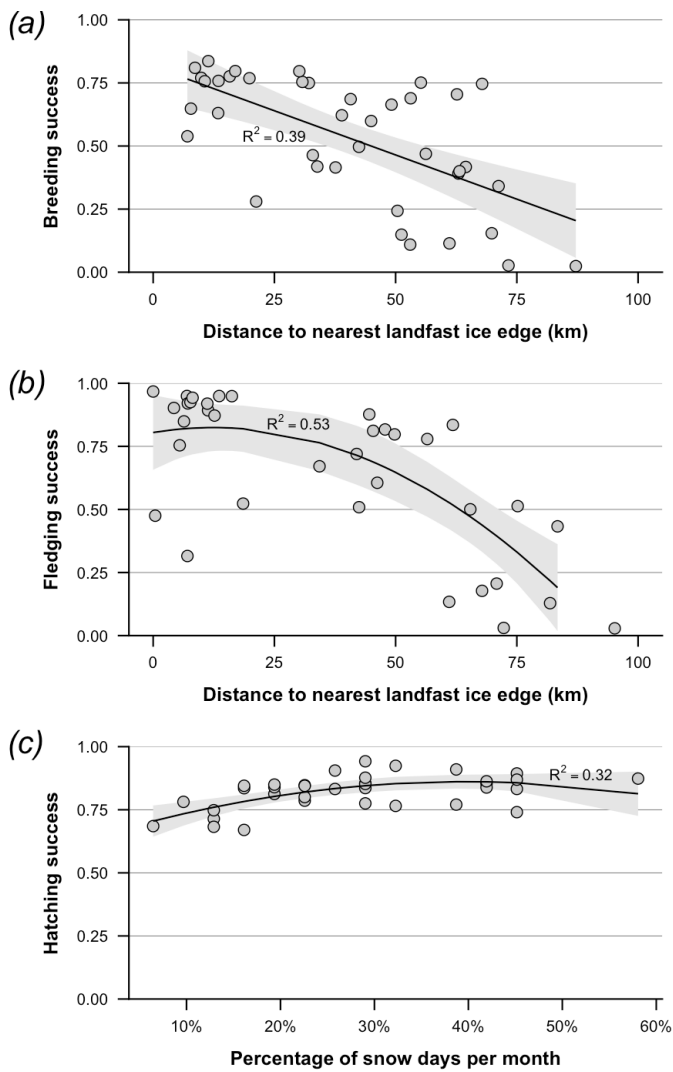
Figures and table

211



212

213 **Fig. 1** Times-series of the emperor penguin reproductive parameters (panel a; 95% confidence intervals in
 214 grey) and LFI conditions (LFIA, panel b; nearest distance to LFIE, panel c) at Pointe Géologie, 1979-2017. Pink
 215 rectangles highlight years for which breeding success was below 25%.



216

217 **Fig. 2** Relationships between emperor penguin reproductive parameters (breeding, fledging, and hatching
 218 successes, panels a, b, and c respectively) and climate variables from 1979 to 2017 at Pointe Géologie obtained
 219 from the climate window analysis. The best climate window was August to November for (a), November for
 220 (b), and May for (c).

221

Table 1. Summary of the climate window analysis.

Climate variables	Biological variable	Period considered	Years	Best climate window	<i>p</i> -value best model ¹	<i>p</i> -value after randomisation	Fit selected [alternative fit]	Sign of the relation	R ² after randomisation (k = 10)
Nearest open water (LFIE)	Breeding success	May-Nov.	1979-2017	Aug.- Nov.	1.48e-05	0.006	linear, AIC = -125.8826 [quadratic, AIC = -125.082]	-	0.386
	Hatching success	May-Aug.	1983-2017						
	Fledging success	May-Nov.	1983-2017	Nov.	x = 0.500 x ² = 0.025	0.035	quadratic, AIC = -107.642 [linear, AIC = -105.3069]	-	0.530
Landfast ice area (136°-146° E)	Breeding success	May-Nov.	1979-2017	NS	0.003	0.499		NS	
	Hatching success	May-Aug.	1983-2017	NS	0.007	0.715		NS	
	Fledging success	May-Nov.	1983-2017	NS	0.0001	0.266		NS	
Nb. of days/month with temperatures under -10° C	Breeding success	May-Nov.	1979-2017	NS	NS	/		NS	
	Hatching success	May-Aug.	1983-2017	NS	NS	/		NS	
	Fledging success	May-Nov.	1983-2017	NS	NS	/		NS	
Nb. of days/month with winds above 28 m/s	Breeding success	May-Nov.	1979-2017	NS	NS	/		NS	
	Hatching success	May-Aug.	1983-2017	NS	NS	/		NS	
	Fledging success	May-Nov.	1983-2017	NS	NS	/		NS	
Nb. of days/month with snowfall	Breeding success	May-Nov.	1979-2017	NS	0.044	0.926		NS	
	Hatching success	May-Aug.	1983-2017	May	x = 0.003 x ² = 0.017	0.0003	quadratic, AIC = -198.8435 [linear, AIC = -194.5369]	+ (bell shape)	0.321
	Fledging success	May-Nov.	1983-2017	NS	NS	/		NS	

¹ For quadratic relationships, *p*-values for the linear and quadratic terms are given as x and x² respectively.

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230

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234

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