Title: Don't get a big head: *Centris pallida* (Hymenoptera: Apidae) male head widths decrease across five decades

Running Title: Declines in male *C. pallida* head width

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Abstract

Historical data suggest that many bee species have declined in body size. Larger-bodied bees with narrow phenological and dietary breadth are most prone to declines in body size over time. This may be especially true in solitary, desert-adapted species that are vulnerable to climate change – such as *Centris pallida* (Hymenoptera: Apidae). In addition, body size changes in species with size-linked behaviors could threaten the prevalence of certain behavioral phenotypes long-term. *C. pallida* solitary bees are found in the Sonoran Desert. Males use alternative reproductive tactics (ARTs) and are dimorphic in both morphology and behavior. *C. pallida* male body size has been studied since the 1970s in the same population. We collected body size data in 2022 and combined it with published records from 1974-2022. We find a persistent decline in the mean head width of patrolling males, and shifts towards smaller body sizes in the populations of males found foraging and hovering. Mating males did not experience a decline in mean body size over time. We discuss hypotheses related to the decline in *C. pallida* male head width. Finally, we advocate for *C. pallida* as an excellent study system for understanding the stability of ARTs with size-linked behavioral phenotypes.

Introduction

Anthropogenic changes in climate and habitat have caused a decline in abundance, a shift in geographic range or phenology, and changes in the morphology, physiology, or behavior of many species, sometimes leading to alterations in life history and ecological relationships (Bartomeus et al. 2011, Biesmeijer et al. 2006, Jacobson et al. 2018, Béltran et al. 2021, Burraco et al. 2020, Chou et al. 2019, Chung & Schulte 2020, Duffy et al. 2015, Huey & Kingsolver 2019, Kuhlmann et al. 2012, Ockendon et al. 2014, Parmesan 2006, Reed 2018, Sinervo et al. 2010, Walters & Hassall 2006, Zattara & Aizen 2021, Sánchez-Bayo & Wyckhuys 2019, Burkle et al. 2013).

Bees may be particularly vulnerable to climate change or habitat modifications. As heterothermic ectotherms they rely on environmental conditions to maintain non-lethal body temperatures (Wieser 1973, Huey & Stevenson 1979). This is compounded by a reliance on resources (e.g., nesting resources, plants) that are often disturbed by human activity (Grab et al. 2019, McCabe et al. 2021). Documented changes in bee populations over time can help determine how human activity may impact bees with different life history characteristics, with knock-on effects for their ecological relationships. (e.g., Cane et al. 2006, Burkle et al. 2013). For example, studies in Europe and the Northeastern regions of North America have demonstrated that larger-bodied bee species are more likely to experience declines in population (Bartomeus et al. 2013, Scheper et al. 2014, Oliveira et al. 2016), or stronger intraspecific declines in body size (Nooten & Rehan 2020, but see Gérard et al. 2019), perhaps due to greater nutritional requirements (Müller et al. 2006).

Bee body sizes have not changed uniformly over time across species, sexes, or regions (Nooten & Rehan 2020, Bartomeus et al. 2013, Scheper et al. 2014, Oliveira et al. 2016, Kleijn & Raemakers 2008), suggesting life history traits and ecosystem characteristics (e.g., habitat fragmentation, Warzecha et al. 2016) may play important roles in determining the impact of human activities on body size. For most bees, body size is determined by resource provisioning in the larval stage (Chole

et al. 2019, Kukuk 1996, Alcock 1984, Lawson et al. 2017), and can thus be strongly influenced by changes in resource availability (Chown & Gaston 2010). Bees with narrow phenological windows and dietary specialists are likely to be more susceptible to declines, given their reliance on a smaller pool of available resources (Bartomeus et al. 2013). Solitary and desert-adapted bees are expected to be particularly vulnerable to climate change (Sala et al. 2000, Loarie et al. 2009, Vale & Brito 2015, Hamblin et al. 2017, Burdine & McCluney 2019, McCabe et al. 2021, but see Silva et al. 2018), given the thermal and hygric stressors already evident in their environment. To date, no studies have tracked changes in morphology of any solitary bees in desert ecosystems.

Declines in body size could also generate species-level behavioral changes whenever size contributes to behavior, such as in many alternative reproductive tactic systems (ARTs). ARTs occur when categorical variation in the morphological/behavioral traits is associated with mating across individuals of the same sex within the same population (Oliveira et al. 2008, Paxton 2005, Shuster 2010). In many such systems, larger- and smaller-bodied individuals use different strategies for accessing mates (e.g., fighters vs. sneakers; Oliveira et al. 2008). Declines in body size may alter the occurrence of size-linked morphs, and their behaviors, resulting in a loss of important intraspecific variation over time.

Centris pallida (Hymenoptera: Apidae) are widespread, common solitary digger bees are found in the Sonoran Desert of the Southwestern United States and Northern Mexico. This species often forms dense nesting aggregations, where many thousands of individuals occupy several hectares. Males emerge first from their natal nests at these sites and use ARTs to find mates. Males are behaviorally and morphologically dimorphic, using different sensory mate location strategies and microclimates (Alcock 1976, Alcock et al. 1977a, Snelling 1984, Barrett et al. 2021, Barrett 2022). Large-morph, 'metandric' males with pale gray coloration patrol in sinuous loops ~10 cm over the emergence site and use scent to locate females emerging from natal nests; males then engage in fights for the

opportunity to dig up and mate with emerging females (Alcock et al. 1976b). Small-morph males, with dark brown coloration, are more behaviorally flexible; they may patrol, but are often found hovering near plants where they use visual cues to locate females or mating pairs flying away from the aggregation site that may be interrupted. Large-morph males have a fitness advantage in situations where mating aggregations are densely populated (Alcock et al. 1977a, 1977b, Alcock 1984, Alcock 1995, Alcock 2013a). *C. pallida* mating aggregations may persist in the same locations over multiple decades – allowing for the continuous resampling of a population (Barrett 2022). *C. pallida* are large-bodied, desert-adapted, solitary bees with an extremely narrow phenological and dietary breadth. Bees nest for less than six weeks in the late spring, and females utilize four species of flowering trees for larval nectar/pollen provisions (*Parkinsonia microphylla, P. aculeata, Olneya tesota*, and, rarely, *Psorothamnus (Dalea) spinosa*; Alcock et al. 1976a). *P. microphylla* is the predominant host plant for *C. pallida* over its entire geographic range (Buchmann, pers. comm). The body sizes of male *C. pallida* have been studied at the same site since for 48 years (Alcock et al. 1977a). By combining historical data on *C. pallida* body sizes from 1974 – 2018 (Alcock et al. 1977a, Alcock 1984, Alcock 1989, Alcock 2013a, Barrett 2022) with data we collected in 2022 from the same population, we aimed to determine if male *C. pallida* bees have experienced persistent changes or persistent stability in body size. Our results demonstrate that the population of males found foraging at trees (representative of the total population of males), hovering, and patrolling have all declined in body size since 1974. However, the population of mating males has not persistently declined in body size over time. In addition, we present the first body size data on female *C. pallida* from this site, for use in future historical comparisons. Finally, we discuss several hypotheses of causes for the decline in male body size, and the implications of declining male body size on the stability of the *C. pallida* ART.

Methods

97 Head width measurements

98 We collected head widths at the same site where most previous research on *C. pallida* body size has
99 been conducted (Alcock et al. 1977a, Alcock 1984, Alcock 1989, Alcock 2013a), in the floodplain by
100 Blue Point Bridge/Saguaro Lake over the Salt River north of Mesa, Arizona (33.552, -111.566).
101 Alcock et al. (1977a) demonstrated that head width is correlated with body weight in *C. pallida* males,
102 and serves as a reliable field indicator of body size.
103 We collected bees (n = 921 males, 114 females) in the same manner as described in Alcock (1984,
104 2013), to be sure our data were comparable. Briefly: for patrolling males, we made rapid sweeps low
105 to the ground with an insect net through open areas of searching males. Digging/fighting males
106 were approached and collected by hand. Foraging males and females were collected with a
107 telescoping insect net as they visited paloverde trees (*Parkinsonia* sp.). Mating males and females were
108 collected while engaged in copulation on the ground or vegetation. Hovering males were collected
109 near mesquite or palo verde trees, wherever they had established stable aerial stations. We measured
110 head widths to 0.01 mm using digital calipers (Wen 10761), before releasing the bees. We collected
111 bees daily when the aggregation was most active between April 20 and May 8, 2022, generally
112 between the hours of 0700 and 1130, and noted the time of collection and behavior for each
113 individual.

114 Historical data for comparisons

115 To obtain historical male head width data, we used reported means and standard deviations in
116 Alcock et al. 1977a, Alcock 1984, Alcock 2013a, and Barrett 2022. Together, these studies report
117 data collected in: 1974, 1975, 1976, 1982, 1988, 2011, 2012, and 2018. As prior surveys of the
118 population by Alcock (et al. 1977; Alcock 1984, 1989, 2013) generally only captured bees between
119 roughly 0700 and 0930, we also used only those bees captured before 0930 in our sampling for the
120 historical comparison with prior literature. Data were also reported for mating, hovering, and

patrolling bees from this site in 2018 (Barrett 2022); however, these bees were collected between 0600 and 1100, with no individual data on time of collection. Patrolling bees in 2018 (Barrett 2022) were not captured in a manner consistent with Alcock's prior surveys, and time of day was shown to impact body size (see results) in patrollers, so we elected not to use the 2018 dataset for patrolling males in the comparison. However, we did include hovering and mating males as they were collected using methods consistent with Alcock's prior surveys and time of day was shown not to impact body size in these populations (see results).

Statistical analysis

Data were analyzed using GraphPad Prism 9.3.1 (GraphPad Prism for Windows 2021). When analyzing data on the total population in 2022 (as compared to the before-0930 dataset used for the historical data comparison), we include all bees captured in 2022 (including males for which we had not taken data on time of capture). Because head width data were not normally distributed for all behavior categories, we used a Kruskal-Wallis test with post-hoc Dunn's MCT to analyze differences between hovering, patrolling, and mating male populations. We used a Mann-Whitney test to compare mating and foraging male populations, and an unpaired t-test to compare digging and fighting males and mean hovering male head widths from 1974/1975 and 2022. We used a linear regression to analyze the effect of time of day on patrolling and hovering male head widths. We also used a linear regression to analyze the effect of year on mean patrolling and mating male head width across studies. All data can be found archived on Dryad.

Results

C. pallida head widths in 2022

We present data on the mean ± SD and ranges of male head widths for the 2022 population of males engaged in: foraging, patrolling, hovering, mating, digging, and fighting behaviors in Table 1.

We also present mean female head widths in this population, for females caught while mating, foraging, or nesting (distribution of female head widths: Supplemental Figure 1).

Table 1. Head widths of *C. pallida* collected in April - May 2022 at Blue Point Bridge before 1130 am (n = 921 male, 114 female).

Type	*Mean ± SD (n)*	*Range*
Foraging Males	4.85 ± 0.36 (203)	4.01 – 5.77
Patrolling Males	5.03 ± 0.34 (410)	4.03 – 5.84
Hovering Males	4.76 ± 0.20 (91)	4.29 – 5.16
Mating Males	5.50 ± 0.31 (71)	4.66 – 6.04
Digging Males	5.48 ± 0.25 (66)	4.74 – 6.00
Fighting Males	5.41 ± 0.25 (71)	4.74 – 5.83
Females	5.23 ± 0.28 (114)	4.33 – 5.95

Hovering males were significantly smaller than patrolling males (Figure 1; Kruskal-Wallis: K-W = 140.4, $p < 0.0001$; Dunn's MCT: $Z = 6.51$, $p < 0.0001$), and both types of males were smaller than mating males (patrolling vs. mating: $Z = 8.70$, $p < 0.0001$; hovering vs. mating: $Z = 11.83$, $p < 0.0001$). Mating males skewed larger than the total population of foraging males (Mann-Whitney test: $U = 1439$, $p < 0.0001$). There was no difference in the mean head widths of digging and fighting males (unpaired t-test: $t = 1.55$, $df = 135$, $p = 0.12$).

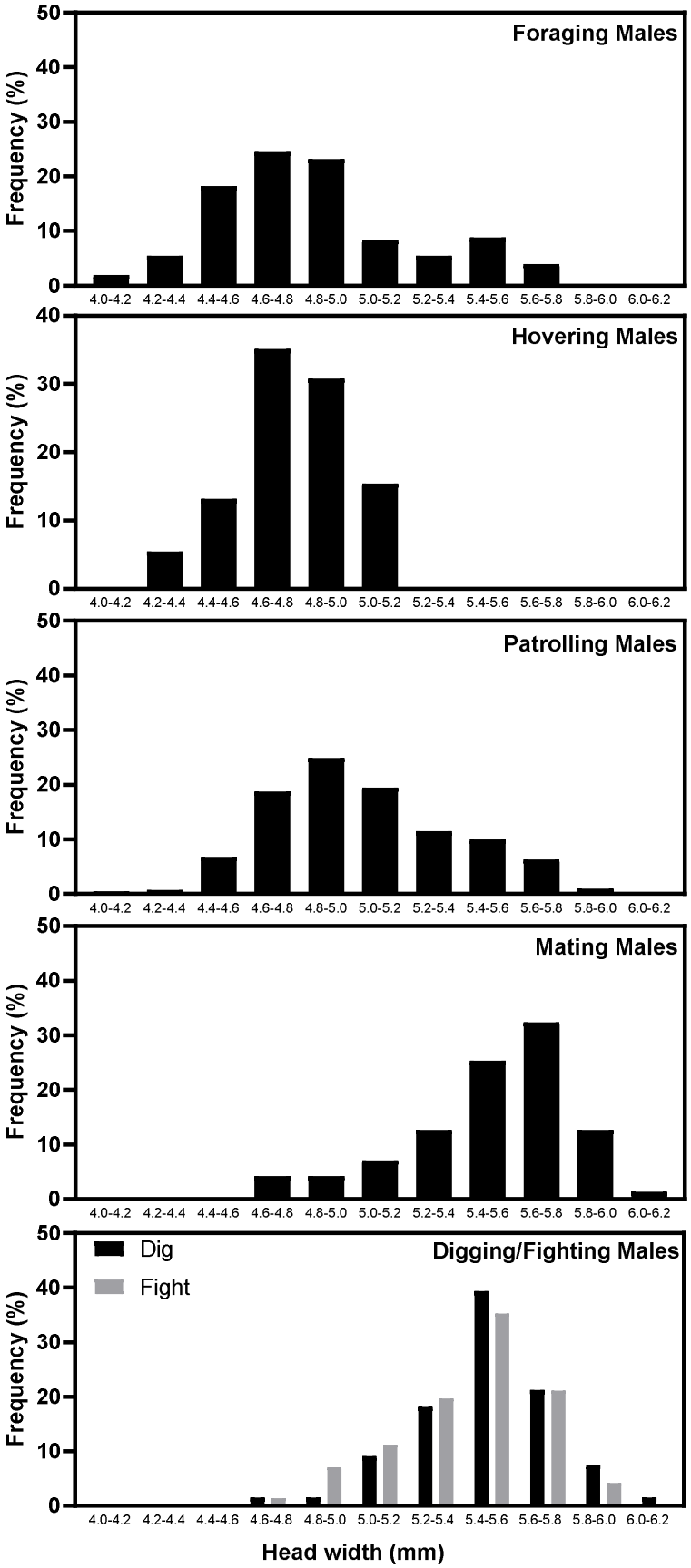

Foraging Males
Hovering Males
Patrolling Males
Mating Males
Digging/Fighting Males
Dig
Fight
Frequency (%)
0
10
20
30
40
50
4.0-4.2
4.2-4.4
4.4-4.6
4.6-4.8
4.8-5.0
5.0-5.2
5.2-5.4
5.4-5.6
5.6-5.8
5.8-6.0
6.0-6.2
Head width (mm)

Figure 1. Distribution of male head widths by behavioral category in 2022. Distribution of male head widths (n = 921) collected while foraging (n = 203), hovering (n = 91), patrolling (n = 410), mating (n = 71), and digging/fighting (n = 66/71) before 1130 on April 20 – May 8, 2022 at Blue Point Bridge, Arizona.

Patrolling and foraging male head widths increased over the course of the morning (Supplementary Figure 2; linear regression, patrolling: [head width] = 0.095 [time of day] + 4.19, F = 23.65, df = 408, R^2 = 0.05, p < 0.0001; foraging: [head width] = 0.097 [time of day] + 4.08, F = 7.90, df = 201, R^2 = 0.03, p < 0.0001); hovering and mating male head widths were constant across the morning (hovering: F = 1.57, df = 88, p = 0.21; mating: F = 0.43, df = 57, p = 0.51).

Historical comparison of mean male head widths from 1974 to 2022

Reported head widths for males foraging, hovering, patrolling, or mating at the Blue Point Bridge site from 1974 to 2022 can be found in Table 2, with associated references for the historical data.

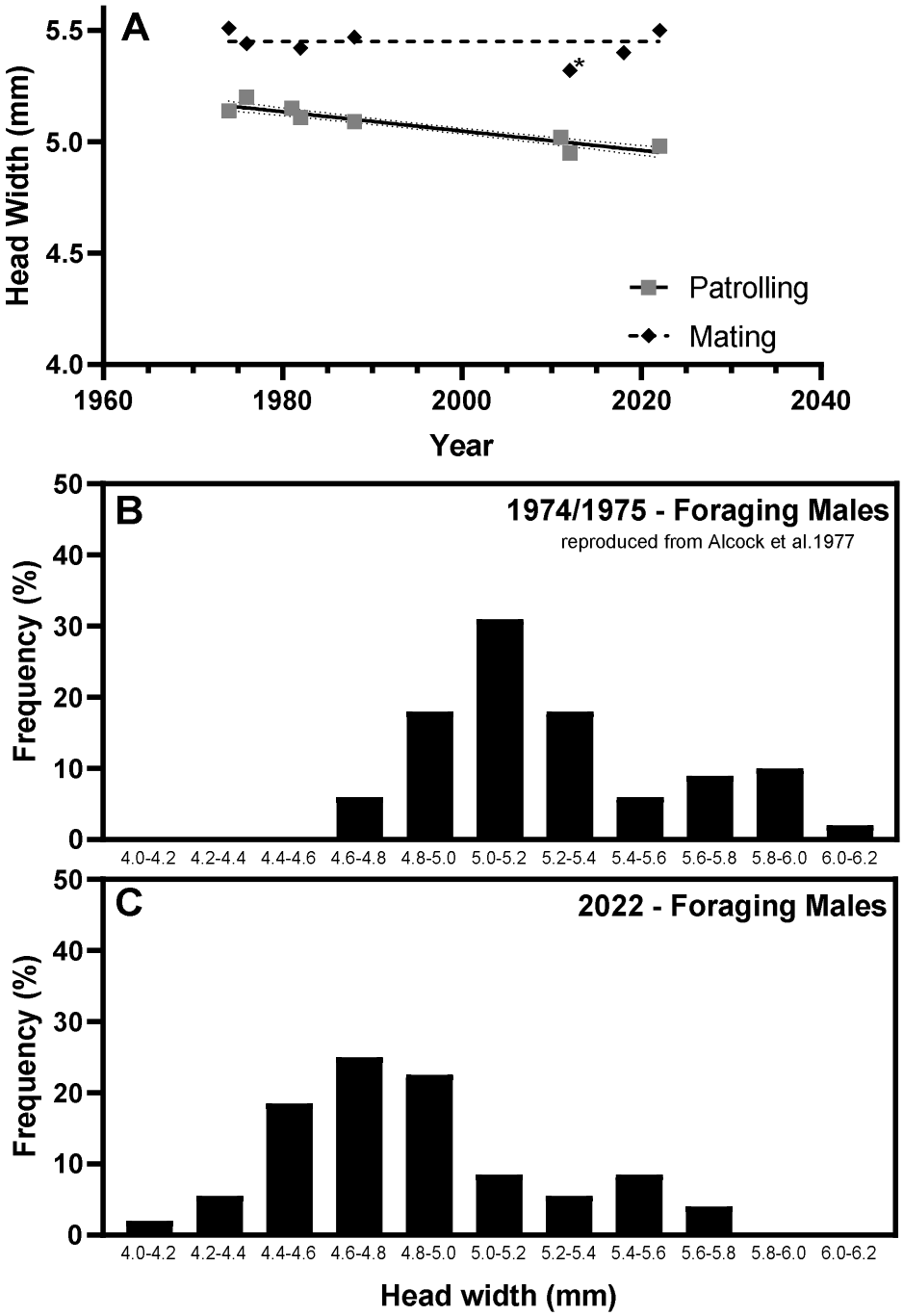
Table 2. Reported means ± SD of males at Blue Point Bridge before 930 from 1974 – 2022.

	Mean ± SD (n)				
Year	Foraging	Hovering	Patrolling	Mating	Reference
1974 + 1975	no mean reported; Supp Fig 3	4.92 ± 0.15 (50)	5.14 ± 0.29 (100)	5.51 ± 0.36 (50)	Alcock et al. 1977a
1976			5.20 ± 0.28 (168)	5.44 ± 0.33 (102)	Alcock 1984, 1989
1981			5.15 ± 0.23 (162)		Alcock 1984
1982			5.11 ± 0.25 (265)	5.42 ± 0.29 (140)	Alcock 1984, 1989
1988			5.09 ± 0.29 (400)	5.47 ± 0.29 (144)	Alcock 1989
2011			5.02 ± 0.28 (214)		Alcock 2013a
2012	4.88 ± 0.31 (132)		4.95 ± 0.25 (285)	5.32 ± 0.29 (11*)	Alcock 2013a
2018		4.86 ± 0.21 (11*†)		5.40 ± 0.31 (23*†)	Barrett 2022
2022	4.84 ± 0.36 (200)	4.77 ± 0.19 (57)	4.98 ± 0.34 (300)	5.50 ± 0.31 (56)	

*small sample size.

170 †these bees were not all collected before 0930, as in the other years, but no individual data on time of capture was recorded. However,
171 body size was not affected by time of day in hovering and mating male populations, so we included these males.
172

173 Patrolling male head widths decreased by 3.72% at the Blue Point Bridge site from 1974 to 2022
174 (Figure 2A, Supplementary Figure 3B; linear regression, [head width] = -0.004344 [year] + 13.74, F
175 = 131.2, df = 1892, R^2 = 0.06, p < 0.0001). Although there were only two years to compare
176 hovering males with a large sample size, there was a significant decrease in mean hovering male head
177 width in 2022 compared to 1974/1975 (Supplementary Figure 3A, unpaired t-test; t = 4.49, df =
178 105, p < 0.0001). The mean of the foraging males (n = 100) measured in 1974/1975 was not
179 reported in Alcock et al. 1977a; however, comparing the distribution of head widths from
180 1974/1975 to our 2022 data suggests significant declines in the head width of the overall population
181 of foraging males (Figure 2B & 2C). Mating male head widths did not change from 1974 to 2022
182 (Figure 2A, Supplementary Figure 4; F = 0.04, df = 524, p = 0.84).



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184 **Figure 2. Changes in head widths of patrolling, foraging, and mating males from 1974 to**

185 **2022.** A) Patrolling male head widths (gray dots, solid line, n = 300) decreased over time at the Blue

186 Point Bridge site from 1974 to 2022 (Figure 2; linear regression, [head width] = -0.004 [year] +

13.74, F = 131.2, df = 1892, R^2 = 0.06, p < 0.0001). Mating male head widths (black diamonds, dashed line to demonstrate non-significance, n = 56) did not change from 1974 to 2022 (F = 0.36, df = 501, p = 0.55). Black dotted lines = 95% confidence interval. *note: small sample size (n = 11) for this year (Alcock 2013a). B) Distribution of head widths of foraging males (n = 100) reported in Alcock et al. 1977a shows larger median head widths than C) the distribution of foraging males (n = 200) collected in 2022. All males collected before 930 am.

Discussion

The mean head width of *C. pallida* males engaged in foraging (e.g., total population), hovering, and patrolling has declined at Blue Point Bridge over the past 50 years. The most frequent head width class has shifted from 5.0 – 5.2 mm in 1974 to 4.6 – 4.8 mm in 2022 (foraging males, Figure 2B,C). Head widths of the mating male population have remained constant over time, despite a significant decline in the frequency of males of this larger size class in the population overall, suggesting that the large-male fitness advantage continues to hold (Alcock et al. 1977a, 1977b, Alcock 1984, Alcock 1995, Alcock 2013a).

Changes in body size over time have been reported for female bees in temperate regions (Bartomeus et al. 2013, Scheper et al. 2014, Oliveira et al. 2016, Nooten & Rehan 2020). Unlike females, males were not reported to decline in body size in the Netherlands; Oliveira et al. (2016) propose that fitness advantages associated with larger male body size may prevent similar declines in males. However, the fitness advantages of larger male body sizes are unclear or nonexistent in many bee species, particularly those without male-male competition (Alcock 2013b). Thus, in combination with our results on *C. pallida,* this seems like an unlikely explanation for the trends observed across bees so far. Further studies in other systems with large-male fitness advantages (Kukuk 1996, Danforth 1991, Alcock 1983, Alcock 1994, Alcock 1997, Paxton 2005) would be beneficial to test this hypothesis.

211 Sex-biased resource allocation is common in many Hymenoptera (e.g., O'Neill & O'Neill 2009),
212 generating male bees that are typically smaller than the females of their species (Shreeves & Field
213 2008). This may help explain the differences observed in male body size trends between *C. pallida*
214 (where this is not the case) and the other studied species in Oliveira et al. (2016). Low quantity or
215 quality larval nutrition significantly reduces survival and impacts adult physiology (Lawson et al.
216 2020, Nicholls et al. 2021), resulting in reduced mating and foraging success (Muller et al. 2015, Xie
217 et al. 2015). The negative fitness consequences of small body sizes may cause a species-specific
218 lower bound on resource allocation per offspring. As male bees are already closer to that species-
219 specific lower bound in resource allocation, this may prevent male bees of most species from
220 declining as much in body size relative to females. *C. pallida* is unique in that males can be the same
221 size or larger than females, allowing for more significant size declines in the male population.
222 Alternately, other life history or ecosystem characteristics between the bees studied in Oliveira et al.
223 (2016) and *C. pallida* may be responsible for variation in reported male body size declines. As a large-
224 bodied, solitary, desert-adapted bee species with narrow phenological and dietary breadth, *C. pallida*
225 may be particularly susceptible to human-activity induced declines. Hypotheses for bee body size
226 declines include: 1) habitat simplification or agricultural intensification, 2) climate-induced
227 phenological mismatches between bees and host plants, or changes in total resource availability (e.g.,
228 lower floral abundance due to more persistent droughts), and 3) increasing temperatures during
229 development (Chole et al. 2019; Sánchez-Bayo et al. 2019). Although we do not test these
230 hypotheses in this report, we provide contextual information that may support particular causes of
231 *C. pallida* body size declines.
232 The area where *C. pallida* have been studied is surrounded by land managed by the United States
233 Forest Service, with minimal development since the 1970s. It is unlikely that habitat simplification or
234 agricultural intensification is responsible for body size declines. Soil significantly buffers ground

temperature fluctuations at 10 cm depth (Parton & Logan 1981, Cane & Neff 2011; approximately *C. pallida* nest depth, Alcock et al. 1976a), which should lessen the impact of increasing temperatures on development and thus body size.

Resource limitation may occur via a combination of phenological mismatch and climate-induced reductions in floral availability. Phenological mismatch, which may arise more frequently for ground-nesting bees with short foraging periods (Stemkovski et al. 2020), is a possible driver of reduced body sizes in *C. pallida*. Though inconsistently documented, it is likely that the emergence dates of *C. pallida* have shifted earlier since the 1970-80s. The female flight season was documented as late May to mid-June in Alcock et al. (1976a); this year (2022), the beginning of the flight season was late April.

More data are available on dates of mating aggregations than female foraging behavior at this site and support the idea of a two week advance in phenology since the 1980s. In 1982, peak emergence is between April 30 – May 14 (Alcock 1984). Peak emergence is even earlier in 2012: Alcock (2013a) suggests peak activity around April 25-May 4. By 2022, we found peak mating between April 20-May 4, an additional five days sooner. Generalist bees in the Northeastern United States have advanced in phenology by ~10 days over the last 130 years, with most of that advance occurring after 1970 (Bartomeus et al. 2011); this aligns with shifts observed in the *C. pallida* mating aggregation activity. However, phenological mismatch is unlikely to be the sole cause of body size declines – studies of native bees have demonstrated that they largely advance at a pace similar to their host plants (Bartomeus et al. 2011). In addition, data on the flowering periods of the three most common host plants for *C. pallida,* collected by the Arizona-Sonora Desert Museum in Tucson from 1983-2009, does not suggest an obvious mismatch in flowering and emergence dates (Arizona-Sonora Desert Museum, 2022).

258 Resource limitation could affect male body size by 1) decreasing female body sizes (maternal and
259 offspring body sizes are linked in *C. pallida*; Alcock 1979) or 2) altering female resource allocation
260 decisions. Unfortunately, no data are available on female *C. pallida* body sizes at Blue Point Bridge
261 prior to 2022, and this relationship is expected to be population-dependent (Alcock 1979). However,
262 body size can affect female flight velocity and pollen carrying capacity (Müller et al. 2006, Everaars
263 et al. 2018), which may have dramatic effects on the number or size of offspring of different types in
264 *C. pallida.* Alcock et al. (1977; Alcock 1979) propose that a females' assessment of the likelihood of
265 nest failure due to parasitism or resource limitation may also affect her decision to allocate for more,
266 smaller (risk-averse strategy) versus fewer, larger male offspring. Notably, resource limitation seems
267 more likely than parasitism: rates of parasitism by bee flies, blister beetles, and mutillids are notably
268 low (Alcock 1979), and no kleptoparasite bees are known to parasitize *C. pallida* nests (Rozen &
269 Buchmann 1990).
270 Irrespective of the mechanism responsible for declines in male *C. pallida* body size, reductions in the
271 frequency of large-morph males over time may have many important consequences for the species.
272 First, the opportunity to pass on genetic information may become increasingly limited to an ever-
273 smaller pool of males capable of winning competitions (the largest males may mate multiple times;
274 Alcock 1995). Second, the stability of the *C. pallida* male ART system, which likely relies on
275 competing selective forces related to nesting density, female provisioning behavior, and male mating
276 success (Alcock 1979), may be threatened by declines in the species's mean body size. The impacts
277 of human activities often consider biodiversity loss at the level of the species, however losses in
278 intraspecific diversity (variation in behavior or morphology) are currently underexplored (see
279 Bolnick et al. 2003). ARTs represent the functional potential a species has to adapt to a changing
280 environment (Oliviera et al. 2016); losses in ecologically functional intraspecific diversity, which
281 might occur if size-based ARTs are destabilized, should be considered when evaluating the impact of

human activities. Additional work following *C. pallida* male and female body sizes at the Blue Point Bridge population may allow for the mechanisms of body size decline in bees broadly, and *C. pallida* specifically, to be further tested, as human-induced climate and landscape modifications continue to drive morphological and behavioral changes in a variety of species.

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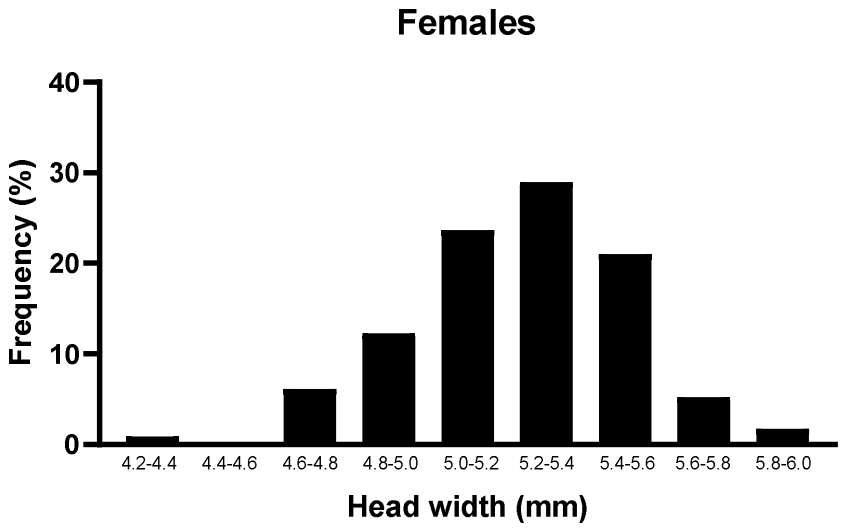
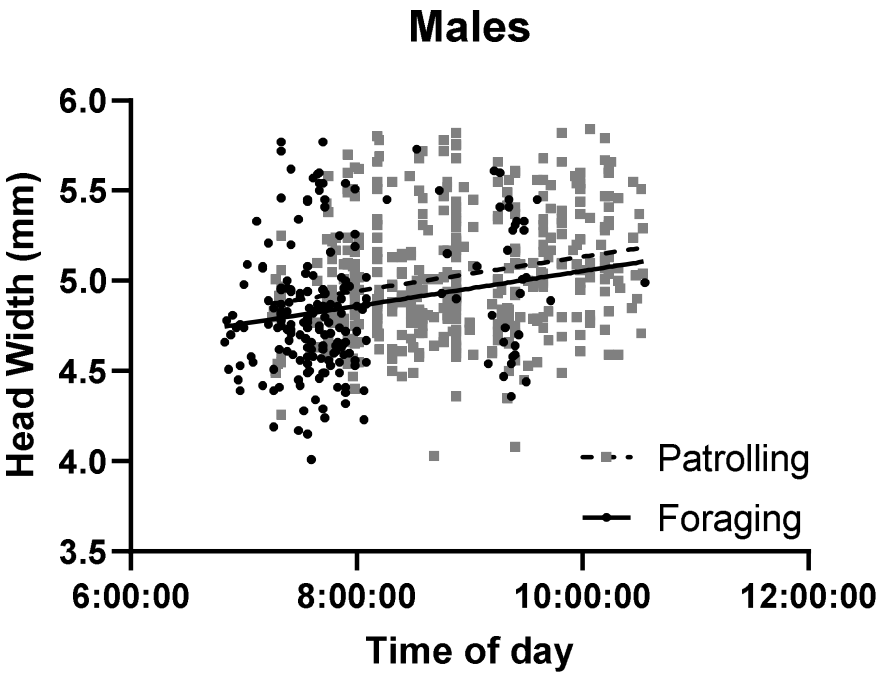
Supplemental Figures

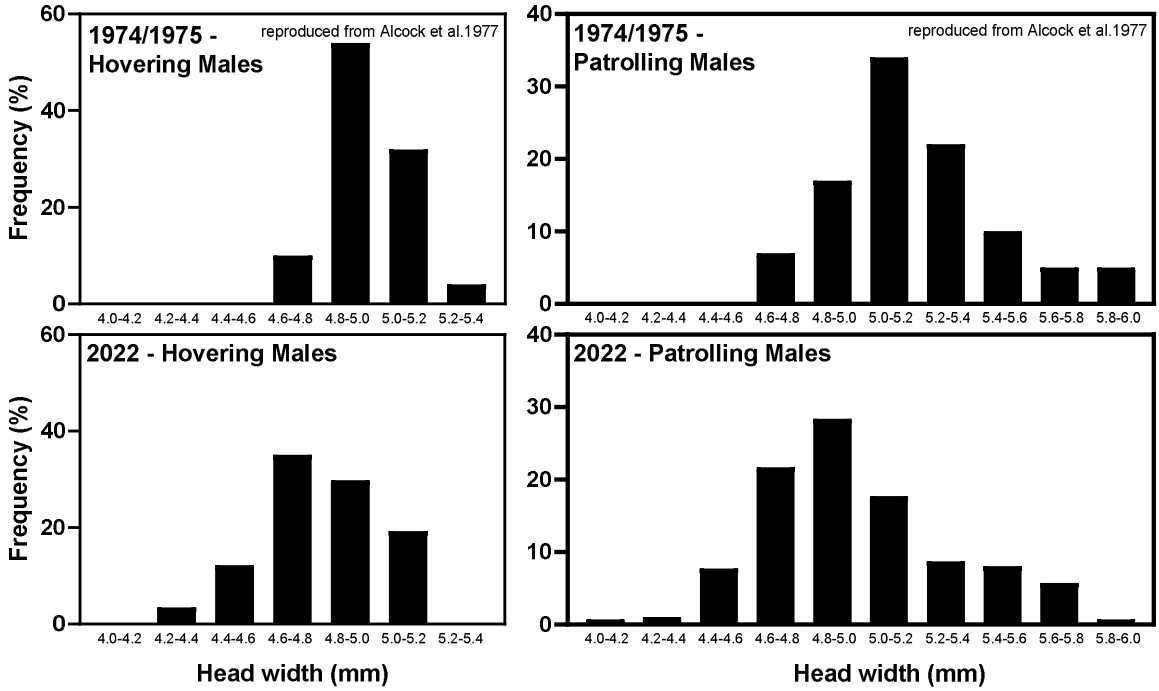


466 **Supplementary Figure 1. Distribution of female head widths in 2022.** Distribution of head
467 widths of females (n = 114) collected while mating, foraging, and nesting from before 1130 on April
468 20 – May 8, 2022, at Blue Point Bridge, Arizona.

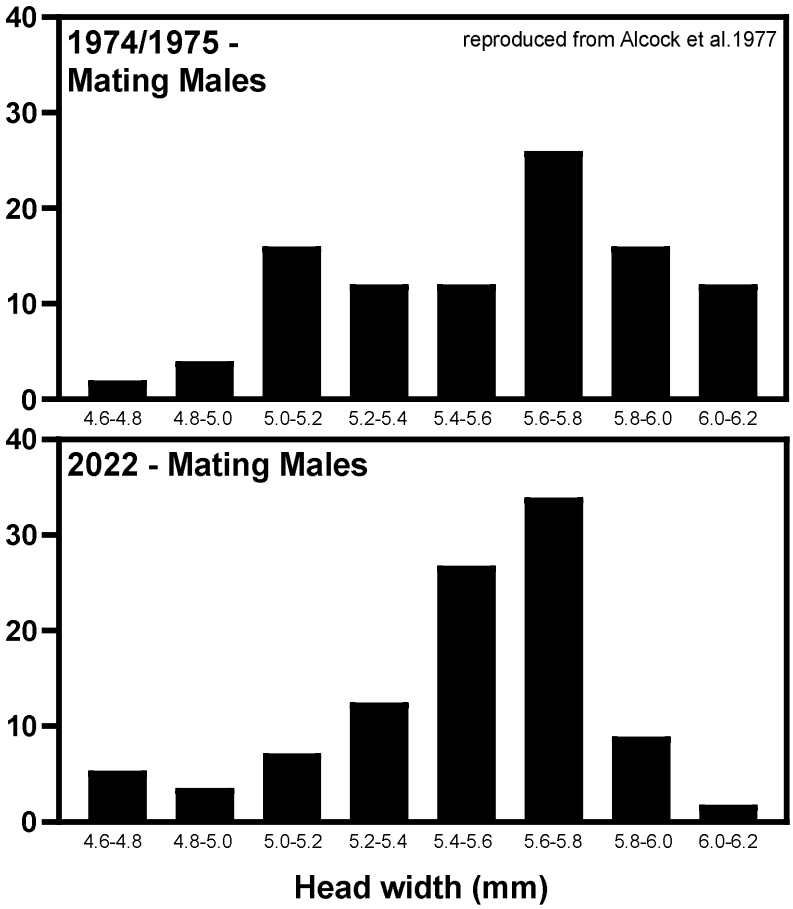


469

470 **Supplementary Figure 2. Increase in patrolling or foraging male head widths from 0700 to**
471 **1130.** Head width in the populations of males patrolling (grey squares, dashed line, n = 410) and
472 foraging (black dots, solid line, n = 203) increased over the course of the morning (Supplementary
473 Figure 2; linear regression, patrolling: [head width] = 0.095 [time of day] + 4.19, F = 23.65, df =
474 408, R^2 = 0.05, $p < 0.0001$; foraging: [head width] = 0.097 [time of day] + 4.08, F = 7.90, df = 201,
475 R^2 = 0.03, $p < 0.0001$).



Supplementary Figure 3. Changes in head width distributions of hovering and patrolling males from 1974 to 2022. Head width distributions for hovering (n = 57) and patrolling (n = 300) males at Blue Point Bridge are skewed towards smaller body sizes in 2022 as compared to 1974/1975 (n = 50 hoverers, 100 patrollers; data reproduced from Alcock et al. 1977a). All males collected before 930 am.



Supplementary Figure 4. Similar head width distributions of mating males from 1974 to 2022. Head width distributions for mating males at Blue Point Bridge demonstrates the population of males that obtain mating opportunities have relatively similar body sizes in 2022 (n = 56) as compared to 1974/1975 (n = 50; data reproduced from Alcock et al. 1977a). All males collected before 0930 am.