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Reduction of the Pectoral Spine and Girdle in Domesticated Channel Catfish is Likely Caused by Changes in Selection Pressure

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1   Reduction of the pectoral spine and girdle in domesticated Channel Catfish is likely caused by

2   changes in selection pressure

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11   **Running Title**: Reduction of Channel Catfish pectoral spines

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16   Tables 1

17   Figures 3

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21   Locked pectoral spines of the Channel Catfish *Ictalurus punctatus* more than double the fish's

22   width and complicate ingestion by gape-limited predators. The spine mates with the pectoral

23   girdle, a robust structure that anchors the spine. This study demonstrates that both spine and

24   girdle exhibit negative allometric growth and that pectoral spines and girdles are lighter in

25   domesticated than in wild Channel Catfish. This finding could be explained by changes in

26   selection pressure for spine growth during domestication or by an epigenetic effect in which

27   exposure to predators in wild fish stimulates pectoral growth. We tested the epigenetic

28   hypothesis by exposing domesticated Channel Catfish fingerlings to Largemouth Bass

29   *Micropterus salmoides* predators for 13 weeks. Spines and girdles grow isometrically in the

30   fingerlings, and regression analysis indicates no difference in proportional pectoral growth

31   between control and predator-exposed fish. Therefore a change in selection pressure likely

32   accounts for smaller pectoral growth in domesticated Channel Catfish. Decreasing spine growth

33   in older fish suggests anti-predator functions are most important in smaller fish. Additionally,

34   growth of the appendicular and axial skeleton is controlled differentially, and mechanical

35   properties of the spine and not just its length are an important component of this defensive

36   adaptation.

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43   Spines have been examined extensively as anti-predator adaptations in a number of aquatic

44   species including *Daphnia* (Tollrian and Dodson 1999) and the Three-Spined Stickleback

45   *Gasterosteus aculeatus* (Huntingford and Coyle 2007). A major adaptation of catfishes, one of

46   the most successful teleost groups, is a hypertrophied first pectoral spine that can be bound and

47   locked (Fine et al. 1997). Binding involves active muscular force that engages friction-locking

48   surfaces between the spine base and the pectoral girdle. Locking requires full abduction of the

49   spine, which traps a spine process within a recess in the coracoid preventing further movement

50   (abduction or adduction). In addition the spine can be rubbed against the cleithrum to produce

51   stridulatory sounds that can serve in distress, agonistic and courtship capacities (Fine and Ladich

52   2003; Kaatz et al. 2010; Parmentier et al. 2010). These specialized functions are mediated by

53   rearranged pectoral muscles (Diogo et al. 2001; Miano et al. 2013) and derived processes

54   (dorsal, anterior and ventral) on the spine base (Hubbs and Hibbard 1951) that mate with

55   complimentary structures on the pectoral girdle (Diogo et al. 2001; Fine et al. 1997). The

56   pectoral girdle (a fused cleithrum, coracoid and scapula) is a robust structure (Fine et al. 1997),

57   providing rigid support for the spine (Schaefer 1984). When locked in a fully-abducted position,

58   the stout pectoral spines of Channel Catfish, *Ictalurus punctatus* Rafinesque more than double

59   the fish's width (Sismour et al. 2013) and impede ingestion by gape-limited predators. Intact

60   Channel Catfish fingerlings are three times less likely to be eaten by Largemouth bass,

61   *Micropterus salmoides* Lacepede than comparably-sized individuals with clipped spines (Bosher

62   et al. 2006), and Largemouth bass consume fewer Channel Catfish than Goldfish, *Carassius*

63   *auratus* L. and Bluegills, *Lepomis macrochirus* Rafinesque in choice experiments, supporting

64   Forbes' dangerous prey hypothesis (Sismour et al. 2013).

3

65 Channel Catfish spines collected beneath eagle nests (Duvall 2007) exhibited subtle

66 morphological differences from those of domesticated stocks (Fine et al. 1997) calling into

67 question the effects of domestication on spine development. Domestication in Channel Catfishes

68 has selected for more rapid growth rate than in natural populations and a reduction of genetic

69 diversity although introduction of new fish has likely minimized inbreeding (Hallerman et al.

70 1986; Smitherman and Dunham 2003).

71 We compared pectoral spines of Channel Catfish from the James River, Virginia with

72 domesticated fish purchased from an Arkansas stock. Smaller spines found in domesticated fish

73 could result from changes in selection pressure over multiple generations. Alternately, exposure

74 to predators in wild fish could induce an epigenetic effect that turns on genes that induce spine

75 growth (phenotypic plasticity). We tested the epigenetic hypothesis by exposing domesticated

76 Channel Catfish fingerlings to Largemouth Bass behind a mesh barrier for several months.

77 Previous work with these individuals demonstrated that fingerlings exposed to Largemouth Bass

78 move and eat less than controls and grow more slowly (Fine et al. 2011). The current study

79 demonstrates that although control fingerlings were longer and heavier than experimental fish,

80 the proportional pectoral spine and girdle weight are similar in control fish and experimental fish

81 exposed to Largemouth Bass, indicating that predators did not induce increased growth of the

82 pectoral skeleton.

83

84 *Methods*

85 Wild Channel Catfish *I. punctatus* were caught by electroshocking (Virginia Department of

86 Game and Inland Fisheries and Virginia Commonwealth University VADGIF permit number

87 0444631 and IACUC AD20216) in the James River, Virginia. Domesticated fish were obtained

4

88   from the aquaculture facility of Virginia State University from stocks purchased from Arkansas.

89   Fish were weighed in grams and measured for total length in mm (TL). Frozen fish were thawed

90   and boiled briefly to clear the skeletons. After drying, pectoral spines were measured for length

91   with digital calipers, and spines and girdles were weighed in milligrams. Since spine tips often

92   break, the longer and heavier spine was used for analysis. Measurements were linearized by log-

93   log transformation, regressed against TL or weight, and regressions of domesticated and wild

94   fish were compared by analysis of covariance. Adjusted means for domesticated and wild fish

95   were calculated from regressions for 400 mm TL and 1,000 g Channel Catfish. Data were plotted

96   on a linear scale to illustrate growth rate.

97   Experimental protocols for non-consumptive effects of Largemouth Bass *Micropterus*

98   *salmoides* predators are provided in Fine et al. (2011) and will be summarized briefly. Juvenile

99   Channel Catfish were measured for total length TL in mm and weighed to 0.1 g. Largemouth

100   Bass (29 to 43 cm TL) were obtained by hook and line from a small impoundment at the Rice

101   Center of Virginia Commonwealth University (Charles City County, Virginia). Fish were

102   maintained in eight 300 L fiberglass tanks at 23 C under a 14:10 LD cycle. A black polyethylene

103   plastic mesh barrier (6.5 mm square openings) was erected across the center of each tank

104   separating them into halves, and a clay flowerpot was added to the catfish side for shelter. Ten

105   Channel Catfish were acclimated in the right half of each tank for one week, after which a

106   Largemouth Bass was added to four of the tanks. Largemouth bass are a generalized fish

107   predator that commonly consumes Channel Catfish in rivers and ponds (Sismour et al. 2013).

108   The other four tanks with no bass served as controls. There was no difference in mean size of

109   control and experimental Channel Catfish at the beginning of the experiment (Fine et al. 2011).

110   Largemouth bass were fed at least twice a week with a dead Channel Catfish from the same

111   stock as the experimental catfish. Catfish were fed to satiation multiple days per week using a

112   standard 32% protein floating-pellet catfish ration. The experiment was conducted for 13 weeks.

113   Based on data from wild and domesticated fish and our hypothesis that predators would

114   increase spine growth, we compared means from control and experimental tanks with a one-

115   tailed T-test. TL, fish weight, pectoral spine length and weight and girdle weight from the four

116   control and four experimental tanks were averaged so that each tank was treated as a unit (N = 4

117   per treatment), and $p < 0.05$ was considered significant. Because of differences in size of control

118   and experimental fish at the termination of the experiment (see results), tank means were not

119   sufficient to determine if relative spine and girdle growth are affected by predators. Growth was

120   therefore evaluated by linear regressions of spine length against fish TL and spine and girdle

121   weight against fish weight. Regressions were compared by analysis of covariance. Because of

122   possible tank effects, we first compared regressions across tanks within control and within

123   experimental treatments. Slopes and intercepts were not significant for spine length, spine weight

124   or girdle weight within either treatment. Since there were no tank effects, data from individual

125   tanks were combined, and relative growth for spines and girdles was evaluated and regressions

126   were compared between control and experimental tanks using individual fish.

127

128   *Results*

129   **PECTORAL COMPARISONS BETWEEN WILD AND DOMESTICATED CHANNEL**

130   **CATFISH**

131   Spine length, spine weight and girdle weight increased continuously with fish size although at a

132   decelerating rate in catfish that ranged from 87 to 562 mm TL (Fig. 1). Adjusted means for

133   domesticated and wild fish respectively were 40.4 and 49.9 mm for spine length, 0.60 and 1.04 g

134　　for spine weight and 5.42 and 7.50 g for girdle weight. Wild catfish had longer and heavier

135　　spines and heavier girdles than domesticated individuals. Slopes for spine lengths did not differ

136　　between domesticated and wild fish ($F_{1,91}$=1.23, p =0.2669), but elevations were greater in wild

137　　fish ($F_{1,92}$=219.6, p<0.0001). Slope for spine weight against fish weight were so much greater in

138　　wild fish ($F_{1,91}$=10.7, p=0.0015) that intercepts could not be tested. Slopes for girdle weight were

139　　similarly greater in wild fish ($F_{1,86}$=8.10, p=0.0055).

140

141　　**PREDATOR EXPOSURE EXPERIMENT**

142　　Mean TL ranged from 16.40 to 17.59 mm for control and 14.38 to 16.06 for experimental tanks

143　　and weights from 37.24 to 45.35 and 21.20 to 31.65 respectively. Control Channel Catfish were

144　　longer (T_6=3.229, p=0.0179) and heavier (T_6=4.384, p=0.0046) than experimental fish at the

145　　termination of the experiment (Fig. 2a, b) indicating that a predator across the barrier retarded

146　　growth (Fine et al. 2011). The control fish had longer (T_6=2.420, p =0.0259) and heavier

147　　(T_6=2.078, p=0.0415) pectoral spines (Fig. 2c, d) as would be expected of larger individuals, but

148　　the difference in girdle weight did not reach significance (T_6=1.808, p=0.1206). In this size

149　　range spines and girdles of both control and experimental catfish grew linearly (Table 1; Fig 3).

150　　The r^2 values for linear regressions of control fish ranged from 0.75 to 0.93 for spine length

151　　against TL, spine weight against weight and girdle weight against weight except for control spine

152　　length against TL with an r^2 of 0.46 (Table 1). Data points for control and experimental fish co-

153　　scattered, and analysis of covariance indicated no significant difference between proportional

154　　pectoral spine length, weight or girdle weight of control fish and fish exposed to Largemouth

155　　Bass (Table 1, Fig 3). The largest individuals were all in control tanks, and these individuals

156　　were likely responsible for slight though not significant differences in intercepts of spine and

7

157   girdle weight regressions. Similar experimental and control regressions indicate that exposure to

158   predators did not increase pectoral growth.

159   *Discussion*

160   The most parsimonious hypothesis to account for the decreased pectoral spine and girdle weight

161   we observed in domesticated fish is changes in selection pressure for this defensive adaptation

162   rather than an epigenetic effect caused by exposure to predators. Domestication of Channel

163   Catfish has involved selection for fast growth in ponds without fish predation, and the pectoral

164   apparatus was not considered when choosing breeding stock (Dunham and Smitherman 1982;

165   Hallerman et al. 1986; Smitherman and Dunham 1993). However, breeding for fast growth

166   could have inadvertently selected for fish with smaller pectoral spines and girdles. We note that

167   spines are not a concern in large commercial ventures since fish are rarely handled individually

168   until processing when they are stunned with a weak electric current before decapitation

169   (Marshall 2004). Additionally smaller spines in aquaculture fish are still an effective adaptation

170   and deter predation by Largemouth Bass (Bosher et al. 2006 Sismour et al. 2013).

171   Relaxation of selection pressure during domestication and inadvertent selection for

172   smaller spines are complimentary hypotheses to explain spine reduction although inadvertent

173   selection might be unlikely in the presence of fish predators. Unraveling the course of selection

174   on spine size will be complex since contemporary aquaculture stocks do not have a single

175   population of origin (Smitherman and Dunham 1983). Therefore, comparisons between cultured

176   stocks with a single wild population of origin would not be possible. Experimentation to confirm

177   either hypothesis could involve developing a cultivated stock from a wild population and

178   following spine development over several generations. Such an endeavor would require at least

179   a decade given that Channel Catfish in Virginia require 4-6 years to mature (Hubert 2000). It

8

180   should also be possible to compare spine size in populations of domesticated fish with different

181   growth rates.

182   Selection pressure on spine length has been demonstrated in populations of *Gasterosteus*

183   *aculeatus* under different predation regimes: populations dominated by fish predators have long

184   spines whereas populations with invertebrate predators have shorter ones (Huntingford and

185   Coyle 2007). Similarly, in Nine-Spined Sticklebacks, a common garden experiment

186   demonstrated that predator density and food availability did not affect body shape or armor,

187   indicating that anti-predator traits are constituitive rather than inducible (Välimäki et al. 2012).

188   The classic example of a predator-induced defense in fishes is an increase in body depth in

189   Crucian carp, *Carassius carassius* (Brönmark and Miner 1992). Similarly, the presence of

190   predators caused morphological changes in perch and roach (Eklöv and Jönssön 2007) and in

191   pumpkinseed sunfish (Januszkiewicz and Robinson 2007).

192   The 13-week experiment reported here resulted in significant growth differences but not in

193   changes in pectoral development when normalized to fish size. Our results do not rule out the

194   possibility of an epigenetic effect on smaller or wild individuals. The negative allometry of

195   pectoral girdle growth suggests that the axial and appendicular skeletons are controlled by

196   different genetic mechanisms. One would expect axial and appendicular skeletons to grow

197   proportionately in most fishes in order to provide normal control of fine movement. Our finding

198   therefore supports the importance of the fused pectoral girdle (Schaefer 1984) as a major

199   component of the anti-predator adaptation provided by the pectoral spines. Furthermore, linear

200   pectoral spine growth in young but not older fish emphasizes the importance of the adaptation in

201   small fish that face increased predation risk. We caution that growth rate in domesticated and

202   wild fish differ.

9

203   The pectoral spine of Channel Catfish is an enlarged flattened fin ray that tapers toward the

204   tip (Fine et al. 1997). The enlarged horizontal profile will increase resistance in the horizontal

205   plane, which opposes forces caused by passage through a predator's mouth or underwater

206   obstructions. Spine and girdle growth is isometric in small juveniles used in this study, and the

207   negative allometry in spine length and weight is due to decreasing growth in larger individuals

208   who would be less vulnerable to predation. Additionally breakage of spine tips occurs commonly

209   in both domestic and wild individuals. Decreasing girdle weight supports a growth effect and not

210   just breakage. The increase in spine weight would be determined by linear dimensions,

211   particularly near the wider spine base, and spine weight per millimeter of spine length increases

212   exponentially with TL (Duvall 2007). Wild Channel Catfish have wider spines (Duvall 2007),

213   which increases the moment of inertia (a greater cross sectional area further from the midline)

214   and therefore breakage resistance of the structure. The larger mass of the pectoral girdle in wild

215   fish is striking since it is a major component of the fish's girth. Finally, the increased spine mass

216   suggests that in addition to spine length (Tollrian and Dodson 1999; Huntingford and Coyle

217   2007) other dimensions that contribute to the material properties of a defensive spine are

218   important to its function.

219   **ACKNOWLEDGMENTS**

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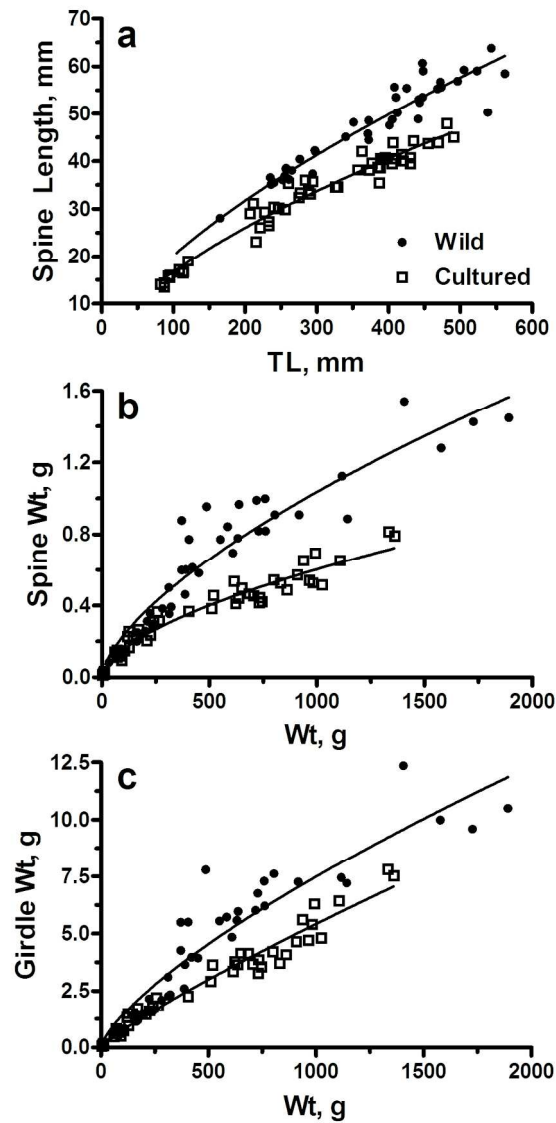
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Figure Legends

Figure 1. Relationship of spine length to total length (a), spine weight to fish weight (b) and pectoral girdle weight to fish weight (c) for wild and domesticated catfish. Equations for James River fish: Log Spine L = 0.001654 + 0.6518 Log TL, r^2 = 0.92; Log Spine Wt = -1.928 + 0.6480 Log Wt, r^2 = 0.89; Log Girdle Wt = -1.284 + 0.7197 Log Wt, r^2 = 0.87. Equations for domesticated fish: Log Spine L = -0.0561 + 0.639, Log TL, r^2 = 0.96; Log Spine Wt = - 1.984 + 0.5885, r^2 =0.96 Log Wt; Log Girdle Wt = - 1.833 + 0.8558 Wt, r^2 = 0.96.

Figure 2. Mean ± SE total length, fish weight, spine length, spine weight, spine length for control and experimental Channel Catfish. * $p < 0.05$, **$p < 0.01$.

Figure 3. Relationship of spine length to total length (a), spine weight to total weight (b) and girdle weight to total weight (c) in control and experimental Channel Catfish.

Relationship of spine length to total length (A), spine weight to fish weight (B) and pectoral girdle weight to fish weight (C) for wild and domesticated catfish. Equations for James River fish: Log Spine L = 0.001654 + 0.6518 Log TL, r2 = 0.92; Log Spine Wt = -1.928 + 0.6480 Log Wt, r2 = 0.89; Log Girdle Wt = -1.284 + 0.7197 Log Wt, r2 = 0.87. Equations for domesticated fish: Log Spine L = -0.0561 + 0.639, Log TL, r2 = 0.96; Log Spine Wt = - 1.984 + 0.5885, r2 =0.96 Log Wt; Log Girdle Wt = - 1.833 + 0.8558 Wt, r2 = 0.96. 120x223mm (300 x 300 DPI)
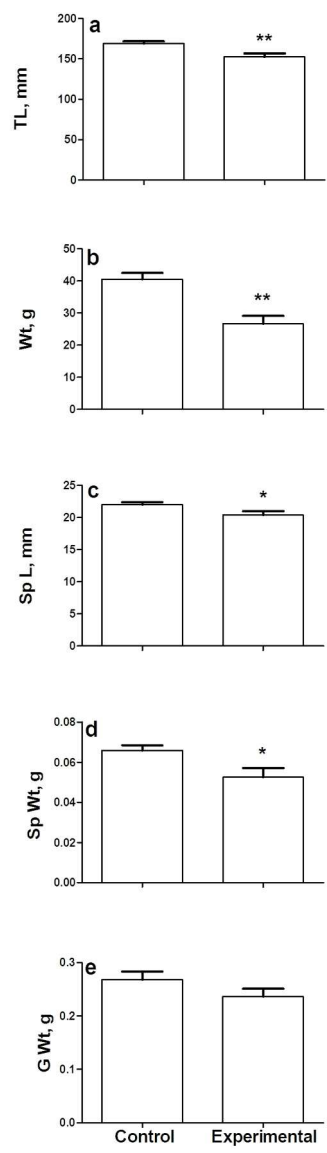
Figure 2. Mean ± SE total length, fish weight, spine length, spine weight, spine length for control and experimental Channel catfish. * p < 0.05, **p < 0.01.
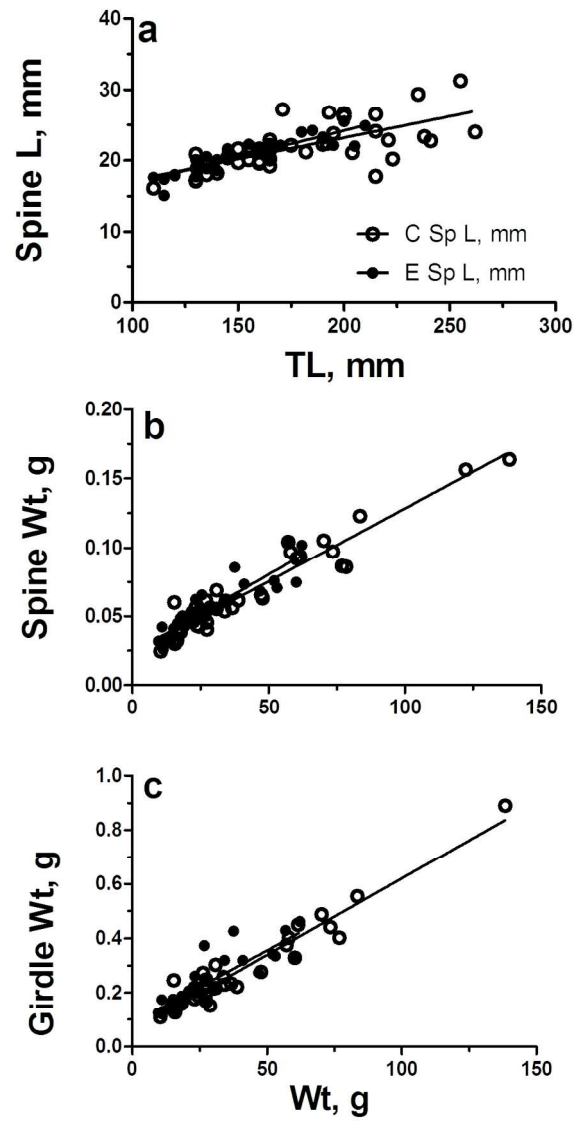72x216mm (300 x 300 DPI)

Figure 3. Relationship of spine length to total length (a), spine weight to total weight (b) and girdle weight to total weight (c) in control and experimental Channel catfish.
113x201mm (300 x 300 DPI)

Table 1 Regression equation and coefficient of determination for spine length against total length, spine weight against fish weight and girdle weight against fish weight, analysis of covariance for slopes and intercepts and adjusted means calculated for 160 mm TL and 50 g weight Channel catfish

Regression Equations	Slope			Intercept		Adjusted Mean
	r^2	F	p	F	p	
Ctrl Spine L=0.0601 TL+11.18	0.46	$F_{1,67}=0.97$	0.32	$F_{1,68}=0.68$	0.41	20.80 mm
Exp Spine L=0.0752 TL+9.168	0.79					21.20 mm
Ctrl Spine Wt=0.0010 Wt+0.022	0.92	$F_{1,67}=0.48$	0.4	$F_{1,68}=2.37$	0.13	0.072 g
Exp Spine Wt=0.0011 Wt+0.023	0.83					0.078 g
Ctrl Girdle Wt= 0.0056 Wt+0.058	0.93	$F_{1,65}=0.14$	0.7	$F_{1,66}=3.57$	0.06	0.338 g
Exp Girdle Wt=0.0054 Wt+0.086	0.75					0.356 g