

Scotland's Rural College

## Causes of keel bone damage and their solutions in laying hens

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2 **Abbreviated title**

3 Keel Bone Damage: Causes and solutions

4 **Summary (100-300 words)**

5 Keel bone damage (KBD) is a critical issue facing the contemporary laying hen industry  
6 due to the likely pain leading to compromised welfare and reduced productivity. Recent reports  
7 suggest that KBD, while highly variable and likely dependent on a host of factors, extends to all  
8 housing systems (including traditional battery cages, furnished cages and non-cage systems),  
9 genetic lines, and management styles. Despite the extent of the problem, the research  
10 community remains uncertain as to the causes and influencing factors of KBD. To combat  
11 these issues, the current review was produced following discussions from the 1<sup>st</sup> International  
12 Keel Bone Damage Workshop held in Switzerland in April 2014. This endeavor sought to  
13 assess current knowledge, foster novel collaborations, propose unique methodologies and  
14 highlight the key areas where innovative research is needed. The current paper is based on the  
15 content of those discussions and presents nine recommendations for future research efforts.

16 **Keywords: Keel, fracture, damage, welfare, bone, laying hen**

17 **Introduction**

18 The high frequency of damage seen in the keel bone (a bone extending from the sternum)  
19 of laying hens within commercial systems represents one of the greatest welfare problems  
20 facing the industry as suggested by the UK's Farm Animal Welfare Committee (FAWC, 2010,  
21 2013). Beyond the obvious welfare issue of gross skeletal deformity, concern stems from the  
22 likely associated pain indicated by the decreased latency to descend from a perch (Nasr *et al.*,  
23 2012a; c, 2014). One type of KBD, keel fractures (KF), also referred to as old breaks, can be  
24 defined as breaks in the bone that will typically manifest as a callus around the fracture site after

25 a few days; KF may also involve sharp, unnatural deviations, or bending, of the bone (Wilkins  
26 *et al.*, 2004). The problem of keel damage is clearly widespread with similar yet highly variable  
27 levels reported in various countries (such as: Switzerland (Kappeli *et al.*, 2011); UK (Wilkins *et*  
28 *al.*, 2011); The Netherlands, Belgium, Germany (Rodenburg *et al.*, 2008; Heerkens *et al.*,  
29 2013); and Canada (Petrik *et al.*, 2014)). Keel bone damage (KBD) extends across genetic lines  
30 (Kappeli *et al.*, 2011) and all types of housing systems (Wilkins *et al.*, 2011; Petrik *et al.*, 2015)  
31 including organic production systems (Bestman and Wagenaar, 2014). Despite their ubiquity,  
32 the causes and influencing factors of KBD remain largely unknown to the research community,  
33 a circumstance that severely handicaps the development of effective strategies to reduce their  
34 occurrence and severity.

35 To identify critical areas where research is needed and coordinate the multiple ongoing and  
36 future research efforts of laboratories, the International Keel Bone Damage Workshop was  
37 organized by the University of Bern in April 2014. This manuscript serves to highlight the  
38 workshop dialogue and harness the collective energies of the research community towards  
39 reducing KBD in laying hens by formulating key recommendations for forthcoming research.

40 **Recommendation 1 – A uniform methods of evaluating KBD should be employed with**  
41 **relevant criteria to ensure reliability of results.**

42 Currently, evaluating KBD in live birds is principally done by palpation; a method that  
43 originated primarily from two papers (Wilkins *et al.*, 2004; Scholz *et al.*, 2008) which have  
44 since been adopted by a variety of labs. While broadly similar in their classification of damage,  
45 key differences exist and require resolution. Most critically, Wilkins *et al.* (2004) only  
46 discussed KF while Scholz *et al.* (2008) included deviations of the keel (deformations from a  
47 theoretically flat, two dimensional plane; also referred to as curving, bending, etc.) as well.  
48 Given that KF and deviations likely result from different causal factors (i.e., sudden impacts

49 causing large forces vs. sustained and small forces, respectively), this lack of clarity represents a  
50 major obstacle in combining results to allow for comprehensive interpretation of the problem.  
51 The multiple methods in use are a challenge in resolving KBD, hindering our abilities to  
52 compare findings and resulting in needless and inefficient replication. We recommend  
53 development of a uniform assessment of KBD that assesses KF and deviations where each uses  
54 a binary scale of whether damage is present. The system should be developed in concert with an  
55 associated scoring sheet which should be made publicly available to facilitate the amalgamation  
56 of data produced by the labs conducting related research.

57 Beyond defining the presence or absence of damage, identifying grades of severity is also  
58 needed to determine the types of KBD that are a concern. Research that can provide reliable and  
59 consistent markers to classify KBD in grades of severity that are grounded in meaningful  
60 criteria relevant to animal welfare (e.g., pain caused by fracture) and/or other spheres of concern  
61 (e.g. productivity) is essential.

62 We also recommend adoption of training criteria for persons assessing KBD (particularly  
63 by palpation which is more subjective than dissection) to ensure greater reliability of results. A  
64 system employed by assessors with appropriate training can produce results that are more useful  
65 in determining true occurrence of damage and evaluating interventions. The method of  
66 assessment, including free access to a developed scoring form, the described definitions for the  
67 various forms of damage, as well as criteria and training for palpation, is described elsewhere  
68 (Casey-Trott *et al.*, *submitted to Poultry Science*).

69 **Recommendation 2 – Investigate low energy, non-collision events as a source of KF.**

70 High energy events within non-cage systems provide a likely mechanism for KF that have  
71 been suggested to result from collisions with elements of animal housing such as perches (Scott  
72 *et al.*, 1997; Moinard *et al.*, 2004a; Sandilands *et al.*, 2009; Wilkins *et al.*, 2011). Counter-

73 intuitively, KF also frequently occur in cage systems where there exists seemingly limited  
74 opportunities for dynamic loading as might occur during collision. Thus, improving our  
75 understanding of the sources of KF will require insight of dynamic as well as static events. The  
76 mechanisms of KF in cage systems are likely not exclusive to this environment, i.e., static  
77 mechanisms are likely to cause damage in non-cage systems as well, and thus deserve  
78 investigation to provide a more comprehensive understanding of the sources of KBD.

79 Although commercial laying hens kept in enriched cages and non-cage systems have  
80 opportunities for weight-bearing activities, birds' skeletons remain fragile because of a  
81 combination of nutritional, environmental and genetic factors (Whitehead, 2004a). It would be  
82 worthwhile to test whether seemingly innocuous, quasi-static activities can induce KF. While  
83 perching, hens place considerable forces on their keels which is in contact with the perch (Pickel  
84 *et al.*, 2011) and certain perch designs or material may result in severe keel bone deviations and  
85 perhaps also KF (Pickel *et al.*, 2010). This mechanism would be similar to compression fractures  
86 in osteoporotic bones of humans, which have been shown to occur spontaneously or with  
87 normally innocuous activities, such as sneezing or twisting (Kondo, 2008). Furthermore,  
88 application of modeling techniques, including finite-element models (Tomaszewski *et al.*, 2010)  
89 that represent the keel bone, would be useful to provide an understanding of the static and  
90 dynamic loading patterns in the bone.

91 More generally, a broader understanding of the keel, using a comparison of relevant bird  
92 phylogenies, could be helpful to establish the morphological capacity of the keel and how  
93 modern housing conditions exceed that capacity. It would be useful to assess keel integrity in  
94 relation to the functional morphology of diverse avian clades that exhibit significant variation in  
95 hindlimb/forelimb modules, keel morphology, flight style, and use of natural perches (Heers  
96 and Dial, 2012).

97           **Recommendation 3 – Investigate the relationship between deviations and KF.**

98           A keel with deviations may lead to unequal bone loading during wing-flapping and  
99           concentration of strain energy in ways that increase the risk of fracture. The paired *pectoralis*  
100           muscles are capable of generating enormous force, work and power output during normal flight  
101           (Tobalske *et al.*, 2003) and these outputs increase dramatically during vigorous wing-flapping  
102           (Tobalske and Dial, 2000; Jackson and Dial, 2011). Comparable wing-flapping is often observed  
103           in commercial laying hens that slip from a perch or aviary tier and try to regain their footing  
104           (personal observation, M Toscano). Three-dimensional force-balance calculations (Hutchinson *et*  
105           *al.*, 2005; Baier *et al.*, 2006) should be used to test for effects of keel deformity upon bone  
106           loading during *pectoralis* muscle contraction; particularly those observed during episodes where  
107           balance is lost or panics (see Recommendation #5). Also, deviated keels may lead to KF  
108           indirectly by complicating balance maneuvers, an additional topic which deserves investigation.

109           **Recommendation 4 – Investigate the role of bird development in KBD susceptibility.**

110           It is of prime importance to learn more about development of locomotor and cognitive skills  
111           as these contribute towards the ability of hens to navigate within the home system. It is doubtful  
112           that the traditional aviary rearing system, where chicks are kept confined to platforms for the first  
113           four weeks after which the sides are opened, is the best system to prepare birds for aviary housing  
114           (Kozak *et al.* 2015). Under natural conditions, locomotor capacity is critical in Galliformes as  
115           they are confronted with immediate challenges to escape predators, search for food and seek  
116           shelter (Dial and Jackson, 2011). Beginning at six days post-hatching, wild Galliformes will  
117           readily flap their wings to produce aerodynamic forces that enhance hindlimb function while  
118           moving up inclines, a behaviour called wing-assisted incline running (WAIR) (Dial, 2003;  
119           Tobalske and Dial, 2007; Dial *et al.*, 2008). Adult Galliformes may also prefer WAIR rather than  
120           flight to reach an elevated area in a complex, natural habitat as well (Dial and Jackson, 2011). A

121 better understanding of this process in commercial strains could be helpful to design juvenile  
122 and/or adult hen housing systems that improve locomotor abilities (Le Blanc et al. 2015). For  
123 instance, variable-engineered systems would be suitable for accommodating the birds as they  
124 develop, using more ramps and adjustable angles with increasing age. A potential advantage of  
125 WAIR compared with flight may be that whole-body kinetic energy is less during WAIR  
126 (Tobalske and Dial, 2000, 2007), a benefit that could reduce the risk of KBD due to accidental  
127 impact with the housing environment. Additionally, increased wing-flapping during development  
128 may assist in improving balancing abilities (Filipa *et al.* 2010) while greater activity is known to  
129 correlate with bone strength (Rath *et al.*, 2000). Beyond musculo-skeletal development, juvenile  
130 birds using WAIR will likely learn neuromuscular coordination that will be useful for negotiating  
131 three-dimensional structures in adulthood, an impairment suggested by Gunnarsson *et al.* (2000).  
132 Research in this area will help to identify optimum rearing conditions likely to protect birds from  
133 cognitive impairment in adulthood.

134 **Recommendation 5 - Investigate the role of escape reactions as a source of KF.**

135 Efforts should also be made to understand the damage resulting from sudden escape  
136 reactions, or panics. Escape is normally triggered by a situation that is, or is perceived to be, life-  
137 threatening and thus is not “normal” in the context of commercial poultry husbandry, though has  
138 been documented (Richards *et al.*, 2012). Escapes resemble the pattern seen in Galliformes  
139 involving take-off using high-frequency, high-amplitude wing beats that feature enormous power  
140 output (Tobalske and Dial, 2000; Tobalske *et al.*, 2003), a quick return to the ground using a  
141 glide, and then resumption of walking or running. Given that the response is one of last resort, its  
142 manifestation is likely to exceed the keel’s morphological capacity. Additionally, escape flights  
143 will not allow for the precise navigation required in housing systems. A more thorough

144 understanding of the causes of escapes is necessary, including the roles of genetic selection and  
145 stockmanship, and the effects of dim lighting conditions and intra-bird spacing (Tillmann, 2009).

146 A comparative evolutionary approach could further aid investigation regarding the role of  
147 escape reactions as a source of damage. A museum survey of wild birds of different species  
148 showed that 4.5% out of a sample size of 6,212 specimens had sustained and survived bone  
149 injuries of which clavicle injuries were the greatest in number, especially in smaller birds,  
150 and were attributed to collisions with solid objects (Tiemeier, 1941). The sample included 45  
151 birds in the Phasianidae, the family that includes the chicken, with an incidence rate of 10% in  
152 this family. These percentages are far lower than incidence rates of KBD in layer hens, but they  
153 do suggest that the escape flight of birds in the Phasianidae (Tobalske and Dial, 2000) may be  
154 correlated with bone damage. An alternative explanation, however, is that some damage reported  
155 by Tiemeier (1941) was due to gunshot, as many species in the Phasianidae are gamebirds.

156 **Recommendation 6 - Investigate genetic capacity to reduce KBD.**

157 The role of genetics as a contributing factor in KBD dates back to work by Hyre (1955)  
158 who showed that the tendency to develop keel deformities was heritable by successfully  
159 selecting for and against KBD over six generations. Even earlier, Warren (1937) showed that  
160 crooked keel bones (in comparison to straight keels) had a reduced ash content which he  
161 suggested was a causal factor. In considering the scope for genetic selection against KBD, we  
162 must first determine what traits should be selected where possibilities include: stronger bones,  
163 improved physical ability, and increased docility. Alternatively, as KBD is a relatively complex  
164 trait with a number of genetic and environmental factors playing a role, genomic selection  
165 should be considered (Fulton, 2012) by carefully monitoring the incidence of KBD in a large  
166 population of laying hens and then comparing genomic information of hens with and hens  
167 without KBD. One of the strengths of this approach is that it does not target a single factor, e.g.



168 bone strength, but focuses on the actual presence or absence of damage. In theory, the  
169 associated mechanism(s) is (are) selected in the process of identifying birds with the desired  
170 trait. A challenge with the genomic approach is that it requires a large sampling population  
171 (e.g., >5,000) of which a clear KBD phenotype is needed. However, once the genomic  
172 fingerprint of a hen with no KBD is acquired, no further phenotypic measurements are required  
173 for the selection program (Eggen, 2012). Although breeding for reduced KBD is attractive, one  
174 should be aware of possible linkages and trade-offs with other traits, e.g., reduced egg shell  
175 thickness and egg breaking strength (Stratmann *et al.*, *in prep*). Whitehead (2004b) provides an  
176 excellent review of the relationship between skeletal integrity and egg quality.

177 **Recommendation 7 – Investigate housing adaptations that affect frequency of KBD.**

178 Large differences between housing systems in the incidence KF indicate that housing  
179 design and/or management plays a key-role (Rodenburg *et al.*, 2008; Wilkins *et al.*, 2011).  
180 Perches have received particular attention. As an indication that perches have a causal role in the  
181 occurrence of KBD, higher rates were reported at end of lay for hens in conventional cages with  
182 (92%) compared to those without (83%) metal perches (Hester *et al.*, 2013). Similarly, Wilkins *et*  
183 *al.*, (2011) reported a 10-34% increase in KF when perches were added in an organic mobile  
184 system. Often, round metal perches are used, which may not offer hens adequate support for their  
185 grip. Perches with slightly larger diameters and those made from more flexible materials (wood,  
186 rubber) have been suggested to be more capable of absorbing forces during impact and  
187 preventing KBD (Pickel *et al.*, 2010, 2011). Perches covered with a soft rubber layer were  
188 successful in reducing the number of keel fractures within a commercial aviary suggesting the  
189 benefit of this option (Stratmann *et al.*, Accepted to PlosONE), possibly not only by reducing the  
190 pressure on the keel, but also by providing a cushion and improved grip when landing (Scholz *et*  
191 *al.*, 2014). Perches as a source of fracture is discussed in more detail by Sandilands *et al.* (2009).

192           Apart from perches, the three-dimensional environment of the hens has to be designed so  
193 that it allows the hens to navigate between the different parts of the system. In most commercial  
194 aviary systems, improvements are possible that would improve hens' possibilities for safely  
195 navigating through the system. One option is to add ramps to aid transition between tiers.  
196 Stratmann *et al.* (2015) showed that adding ramps to a commercial aviary system reduced falls  
197 by 55%, collisions by 41% and keel fractures by 24%, while movements between tiers  
198 increased by 44%. The width of the corridors between the different rows within systems also  
199 needs further attention. If the corridor width is at the limit of the birds' navigational ability, it  
200 may cause increased collisions due to misjudged jumps (Heerkens *et al.*, 2014).

201           Another factor to be considered when determining optimum housing is lighting. In many  
202 commercial laying hen operations, light intensity is kept at a relatively low level, especially in  
203 flocks that are prone to develop feather pecking. Birds need sufficient light and contrast to make  
204 an appropriate jump and safe landing (Moinard *et al.*, 2004b). The timing of the light transition  
205 also seems important: Stratmann *et al.* (2013) reported that vertical movements occurred mainly  
206 during a dusk phase when hens usually move to a perching spot for the night. A sudden switch  
207 from light to dark periods may increase the risk of KF during this time. Hence, a gradual dawn-  
208 and dusk should be investigated as a possible means of reducing KF. Lastly, Heerkens *et al.*  
209 (2014) found flooring type to also be a factor where wire flooring had greater frequency of KF  
210 compared with plastic flooring, though the underlying causes need to be explored.

211           **Recommendation 8 – Investigate nutritional solutions to reduce KBD.**

212           Solutions should also include changes in bird management and nutrition. The high  
213 incidence of KF in cages (Hester *et al.*, 2013) could point to a calcium shortage. Egg shell  
214 formation takes place during the night and hens need a large amount of calcium at this time to  
215 produce an eggshell each day. Hens can mobilize this calcium partly from their bones, but they

216 need to restore their supply, otherwise the risk osteoporosis (Whitehead and Fleming, 2000).  
217 One way to supply hens with calcium during the night is to give them daytime access to calcium  
218 sources with larger particle sizes, such as grit or shells, which will then be digested during the  
219 night. Larger particle sizes of calcium has been shown to benefit skeletal health (Cheng and  
220 Coon, 1990; Guinotte *et al.*, 1995) including that of the keel (Fleming *et al.*, 1998), though  
221 usage of this technique varies due to multiple factors including damage to feeding equipment  
222 and birds selectively eating the larger particles. Thus, there may be a benefit in supplying grit  
223 separately, or developing other sources of calcium that help the hens to restore their supplies  
224 and prevent bone weakness. Other nutritional changes could involve incorporation of omega-3  
225 content into the diet which has been shown to result in reduced fracture incidence (Toscano *et*  
226 *al.*, Accepted to Poultry Science; Tarlton *et al.*, 2013) possibly by modulating bone metabolism  
227 and modeling (Liu *et al.*, 2003; Watkins *et al.*, 2003; Baird *et al.*, 2008).

#### 228 **Recommendation 9 – Investigate and quantify KBD and production losses**

229 Physical conditions that are associated with pain can, if severe enough, induce redistribution  
230 of endogenous resources and derail physiological processes that ensure long-term survival, a  
231 classical criterion for compromised welfare (Moberg, 1985; Broom, 1991). More specifically,  
232 Prunier *et al.*, (2013) advocated changes in productivity as an indication of pain and potentially  
233 for compromised welfare. As mentioned before, recent work has shown that individual birds  
234 with fractures housed in large groups (~350 birds/group) produced eggs that were characterized  
235 with reduced breaking strength and thinner shells (Toscano, *in prep*). This response may  
236 represent a diversion of resources where minerals (e.g. calcium) and energy, normally directed  
237 towards egg production, must consequently be reallocated to the process of healing bone  
238 (Thiruvankadan *et al.*, 2010). Similar results for altered egg production in individual birds were  
239 found by Nasr *et al.* (2012b, 2013), although this was assessed in non-commercial conditions

240 (i.e., individual hens isolated in separate cages) in order to link the egg and hen. More critically,  
241 work by Nasr *et al.* (2012b, 2013), as well as that by Toscano (*in prep*), did not control for  
242 natural variation in bird laying capacity. The lack of pre-KF data leaves open the possibility that  
243 birds prone to KF may produce less and weaker eggs independent of whether KFs occurred.  
244 Differences in egg character after fracture must be shown to be absent beforehand if the  
245 measure is to be a valid indicator of welfare. Interestingly, others have been unable to  
246 demonstrate a link between egg production and keel fracture at the flock level (Heerkens *et al.*,  
247 2013). The lack of a relationship could be due to high flock-level variance rather than the  
248 absence of an effect, indicating the need for research at bird level responses. Alternatively,  
249 Whitehead (2004b), reviewing several studies that examined individually housed birds bred for  
250 different bone qualities, suggested that little correlation existed between egg production and  
251 bone quality. The finding was supported by Gebhardt-Henrich and Fröhlich (2012) who  
252 reported more fractures in hens which laid their first egg earlier. As an additional complication  
253 in linking the occurrence of fractures with production data, the period in which fractures are  
254 seen to most dramatically increase (25 -35 weeks of age) is also the one in which birds are  
255 coming off peak of lay, thus a drop in production is expected independent of fractures.  
256 Therefore, the predicted falloff in egg production resulting from KBD may be subsumed by the  
257 drop in egg production as the hen exits the peak of lay period.

258 As discussed above, quantification of production endpoints and the loss of productivity  
259 associated with KBD can be used as a powerful means to assess changes in animal welfare.  
260 More so, because concern for animal welfare is not globally consistent (Lopez, 2007) with the  
261 strongest interest in Europe and North America, framing the problems of KBD in terms of  
262 productivity losses and compromised profit could provide alternative motivations that move  
263 towards an ultimate goal of reducing KBD. This particular argument is powerful as it does not

264 diminish the reality that action on the grounds of compromised welfare is necessary, but rather  
265 adds a supplementary dimension that will drive stakeholders to effect change.

266 Interestingly, it is often suggested that KF result from bone that is weakened by the process  
267 of demineralization to provide adequate amounts of calcium for egg shell formation. If correct,  
268 continued egg production should associate with a decrease in bone strength and an increase in  
269 the occurrence of KF. While this appears to be the case for the first 20 weeks of egg production,  
270 recent comparisons of several studies suggest that rates of fractures actually appear to flatten  
271 and possibly fall after 45 wks of age (Stratmann et al., accepted to Applied Animal Behaviour  
272 Science; Toscano et al., accepted to Poultry Science; Tarlton et al., 2013; Petrik et al., 2014). It  
273 is possible that this decrease could be attributed to altered behaviour, though use of an *ex vivo*  
274 impact testing protocol with dead hens (Toscano *et al.*, 2013) identified a pattern of decreased  
275 susceptibility to fracture (Toscano *et al.*, 2014) that mirrored the on-farm observations of live  
276 hens. Further research is needed to determine how this change in fracture occurrence relates to  
277 altered bone physiology and egg production during this period.

## 278 **Overall Conclusions**

279 Keel bone damage represents a welfare and productivity problem for the laying hen  
280 industry and, while achievements have been made in understanding the nature and cause of  
281 occurrence, we remain far from resolving the issue. The current paper highlights areas of  
282 research that would achieve the goal of reducing KBD, encourage adoption of methods to  
283 improve the accuracy and reliability of reporting, and provide technical changes that could be  
284 adopted.

## 285 **References**

286 **BAIER, D. B., GATESY, S. M. and JENKINS, F. A.** (2006) A critical ligamentous  
287 mechanism in the evolution of avian flight. *Nature* Vol. **445**: 307–310.

288 **BAIRD, H. T., EGGETT, D. L. and FULLMER, S.** (2008) Varying ratios of omega-6: omega-  
289 3 fatty acids on the pre-and postmortem bone mineral density, bone ash, and bone breaking  
290 strength of laying chickens. *Poultry Science* **87**: 323–328

291 **BESTMAN, M. and WAGENAAR, J. P.** (2014) Health and Welfare in Dutch Organic Laying  
292 Hens. *Animals* **4**: 374–390.

293 **BROOM, D. M.** (1991) Animal Welfare: Concepts and measurements. *Journal of Animal*  
294 *Science* **69**: 4167–4175.

295 **CHENG, T. K. and COON, C. N.** (1990) Effect of calcium source, particle size, limestone  
296 solubility in vitro, and calcium intake level on layer bone status and performance. *Poultry*  
297 *Science* **69**: 2214–2219.

298 **DIAL, K. P.** (2003) Wing-assisted incline running and the evolution of flight. *Science* **299**: 402–  
299 404.

300 **DIAL, K. P. and JACKSON, B. E.** (2011) When hatchlings outperform adults: locomotor  
301 development in Australian brush turkeys (*Alectura lathami*, Galliformes). *Proceedings Royal*  
302 *Society Biological Sciences* **278**: 1610–1616.

303 **DIAL, K. P., JACKSON, B. E. and SEGRE, P.** (2008) A fundamental avian wing-stroke  
304 provides a new perspective on the evolution of flight. *Nature* **451**: 985–989.

305 **EGGEN, A.** (2012) The development and application of genomic selection as a new breeding  
306 paradigm. *Animal Frontiers* **2**: 10–15.

307 **FAWC.** (2010) Opinion on Osteoporosis and Bone Fractures in Laying Hens . *Farm Animal*  
308 *Welfare Council*, London.

309 **FAWC.** (2013) An open letter to Great Britain Governments: Keel bone fracture in laying hens.

310 **FILIPA, A., BYRNES, R., PATERNO, M.V., MYER, G.D., AND HEWETT., T.E.** (2010)  
311 Neuromuscular training improves performance on the star excursion balance test in young female  
312 athletes. *Journal of Orthopaedic and Sports Physical Therapy* **40**: 551-558.

313 **FLEMING, R. H., MCCORMACK, H. A. and WHITEHEAD, C. C.** (1998) Bone structure  
314 and strength at different ages in laying hens and effects of dietary particulate limestone, vitamin  
315 K and ascorbic acid. *British Poultry Science* **39**: 434–440.

316 **FULTON, J. E.** (2012) Genomic selection for poultry breeding. *Animal Frontiers* **2**: 30–36.

317 **GEBHARDT-HENRICH, S. and FRÖLICH, E. K. F.** (2012) Auftreten von  
318 Brustbeinfrakturen und individuelles Verhalten bei Legehennen. ERHARD, M., POLLMAN, U.,  
319 PUPPE, B., REITER, K. and WAIBLINGER, S. (Eds)*KTBL*, pp. 52-60 (Freiburg, Germany).

320 **GUINOTTE, F., GAUTRON, J., NYS, Y. and SOURMARMON, A.** (1995) Calcium  
321 solubilization and retention in the gastrointestinal tract in chicks (*Gallus domesticus*) as a  
322 function of gastric acid secretion inhibition and of calcium carbonate particle size. *British*  
323 *Journal of Nutrition* **73**: 125–139.

324 **GUNNARSSON, S., YNGVESSON, J., KEELING, L. J. and FORKMAN, B.** (2000) Rearing  
325 without early access to perches impairs the spatial skills of laying hens. *Applied Animal*  
326 *Behaviour Science* **67**: 217–228.

327 **HEERKENS, J., DELEZIE, E., KEMPEN, I., ZOONS, J., RODENBURG, T. B. and**  
328 **TUYTENS, F.** (2013) Do keel bone deformations affect egg-production in end-of-lay housing  
329 hens housed in aviaries? TAUSON, R., BLOKHUIS, H. J., BERG, L., ELSON, A. (Eds) *9th*  
330 *European Poultry Conference*, pp.127 (Uppsala, Sweden).

331 **HEERKENS, J. L. T., KEMPEN, I., ZOONS, J., DELEZIE, E., RODENBURG, T. B.,**  
332 **AMPE, B. and TUYTTENS, F. A. M.** (2014) Effect of aviary housing characteristics on laying

333 hen welfare and performance. *Proceedings of the 48th Congress of the International Society for*  
334 *Applied Ethology*, Vitoria-Gasteiz, Spain pp. 158.

335 **HEERS, A. M. and DIAL, K. P.** (2012) From extant to extinct: locomotor ontogeny and the  
336 evolution of avian flight. *Trends in Ecology. and Evolution.* **27**: 296–305.

337 **HESTER, P. Y., ENNEKING, S. A., HALEY, B. K., CHENG, H. W., EINSTEIN, M. E. and**  
338 **RUBIN, D. A.** (2013) The effect of perch availability during pullet rearing and egg laying on  
339 musculoskeletal health of caged White Leghorn hens. *Poultry Science* **92**: 1972–1980.

340 **HUTCHINSON, J.R., ANDERSON, F. C., BLEMKER, S.S. and DELP, S. L.** (2005)  
341 Analysis of hindlimb muscle moment arms in *Tyrannosaurus rex* using a three-dimensional  
342 musculoskeletal computer model: implications for stance, gait, and speed. *Paleobiology* **31**: 676–  
343 701.

344 **HYRE, H. M.** (1955) The effect of heredity and environment on keel deformities in White  
345 Leghorns. *West Virginia Agricultural Experiment Station Bulletin.***381**.

346 **JACKSON, B. E. and DIAL, K. P.** (2011) Scaling of mechanical power output during burst  
347 escape flight in the Corvidae. *Journal of Experimental Biology* **214**: 452–461.

348 **KAPPELI, S., GEBHARDT-HENRICH, S. G., FROHLICH, E., PFULG, A. and**  
349 **STOFFEL, M. H.** (2011) Prevalence of keel bone deformities in Swiss laying hens. *British*  
350 *Poultry Science* **52**: 531–536.

351 **KONDO, K. L.** (2008) Osteoporotic vertebral compression fractures and vertebral augmentation.  
352 *Seminars in interventional radiology.* Thieme Medical Publishers pp. 413.

353 **KOZAK, M., TOBALSKE, B., MARTINS, C., WERBEL, H., and HARLANDER-**  
354 **MATAUSCHEK, A.** (2015) Chick- locomotion in a multilayer environment, accepted in *Poultry*  
355 *Science Association 104rd Annual Meeting*, Kentucky, USA.



356 **LEBLANC, C., TOBALSKE, B., WUERBEL, H. and HARLANDER-MATAUSCHEK, A.**  
357 (2015) Locomotion skills of chicks over an inclined walkway. accepted in *Poultry Science*  
358 *Association 104rd Annual Meeting*, Kentucky, USA.

359 **LIU, D., VEIT, H. P., WILSON, J. H. and DENBOW, D. M.** (2003) Long-term  
360 supplementation of various dietary lipids alters bone mineral content, mechanical properties and  
361 histological characteristics of Japanese quail. *Poultry Science* **82**: 831–839.

362 **LOPEZ, J.** (2007) Animal Welfare: Global Issues, Trends and Challenges. Scientific and  
363 Technical Review, Vol. 24 (2). *Canadian. Veterinary. Journal.* **48**: 1163-1164.

364 **MOBERG, G. P.** (1985) Biological response to stress: Key to assessment of well-being, in:  
365 MOBERG, G. P. (Ed) *American Physiological Society*, pp. 28-49 (Bethesda, MD).

366 **MOINARD, C., STATHAM, P. and GREEN, P. R.** (2004a) Control of landing flight by laying  
367 hens: implications for the design of extensive housing systems. *British Poultry Science* **45**: 578–  
368 584.

369 **MOINARD, C., STATHAM, P., HASKELL, M. J., MCCORQUODALE, C., JONES, R.B.**  
370 **and GREEN, P. R.** (2004b) Accuracy of laying hens in jumping upwards and downwards  
371 between perches in different light environments. *Applied Animal Behaviour Science* **85**: 77–92.

372 **NASR, M. A. F., MURELL, J. and NICOL, C. J.** (2013) The effect of keel fractures on egg  
373 production, feed, and water consumption in individual laying hens. *British Poultry Science* **54**:  
374 165–170.

375 **NASR, M. A. F., MURELL, J., WILKINGS, L. J. and NICOL, C. J.** (2012a) The effect of  
376 two classes of opioid drug on the landing ability of laying hens with and without keel fractures.in  
377 *UFAW Animal Welfare Conference: Recent Advances in Animal Welfare Science III*, York, UK.

378 **NASR, M. A. F., MURELL, J., WILKINGS, L. J. and NICOL, C. J.** (2012b) The effect of  
379 keel fractures on egg production parameters, mobility and behaviour in individual laying hens.  
380 *Animal Welfare* **21**: 127–135.

381 **NASR, M. A. F., MURELL, J., WILKINGS, L. J. and NICOL, C. J.** (2012c) Do Laying Hens  
382 with Keel Bone Fractures Experience Pain? *PLoS One* **7**:e42420.

383 **NASR, M. A. F., MURELL, J., WILKINGS, L. J. and NICOL, C. J.** (2015) The effects of  
384 two non-steroidal anti-inflammatory drugs on the mobility of laying hens with keel bone  
385 fractures. *Veterinary Anaesthesia and Analgesia***42**: 197-204.

386 **PETRIK, M. T., GUERIN, M. T. and WIDOWSKI, T. M.** (2014) On-farm comparison of keel  
387 fracture incidence in conventional cage and floor-housed laying hens. *Poultry Science*  
388 *Association 103rd Annual Meeting*, Corpus Christi, pp. 71

389 **PETRIK, M. T., GUERIN, M. T. and WIDOWSKI, T. M.** (2015) On-farm comparison of keel  
390 fracture prevalence and other welfare indicators in conventional cage and floor-housed laying  
391 hens in Ontario, Canada. Accepted to *Poultry Science*.

392 **PICKEL, T., SCSHOLZ, B. and SCHRADER, L.** (2010) Perch material and diameter affects  
393 particular perching behaviours in laying hens. *Applied Animal Behaviour Science* **127**: 37–42.

394 **PICKEL, T., SCSHOLZ, B. and SCHRADER, L.** (2011) Pressure load on keel bone and foot  
395 pads in perching laying hens in relation to perch design. *Poultry Science* **90**: 715–24.

396 **PRUNIER, A., MOUNIER, L., LE NEINDRE, P., LETERRIER, C., MORMÈDE,**  
397 **PAULMIER, V., PRUNET, P., TERLOUW, C. and GUATTEO, R.** (2013) Identifying and  
398 monitoring pain in farm animals: a review. *Animal* **7**: 998–1010.

399 **RATH, N. C., HUFF, G. R., HUFF, W. E. and BALOG, J. M.** (2000) Factors regulating bone  
400 maturity and strength in poultry. *Poultry Science* **79**: 1024–1032.

401 **RICHARDS, G. J., BROWN, S. N., BOOTH, F., TOSCANO, M. J. and WILKINS, L. J.**  
402 (2012) Panic in free-range laying hens. *Veterinary Record* **170**: 519

403 **RODENBURG, T. B., TUYTTENS, F. A. M., DE REU, K., HERMAN, L., ZOONS, J. and SONCK, B.** (2008)  
404 Welfare assessment of laying hens in furnished cages and non-cage systems : an on-farm  
405 comparison. *Animal Welfare* **17**: 363–373.

406 **SANDILANDS, V., MOINARD, C. and SPARKS, N. H. C.** (2009) Providing laying hens with  
407 perches: fulfilling behavioural needs but causing injury? *British Poultry Science* **50**: 395–406.

408 **SCHOLZ, B., KJAER, J. B. and SRADER, L.** (2014) Analysis of landing behaviour of three  
409 layer lines on different perch designs. *British Poultry Science* **55**: 419-426.

410 **SCHOLZ, B., RÖNCHEN, S., HAMANN, H., HEWICKER-TRAUTWEIN, M. and DISTL,**  
411 **O.** (2008) Keel bone condition in laying hens : a histological evaluation of macroscopically  
412 assessed keel bones. *Berliner und Münchener Tierärztliche Wochenschrift* **121**: 89–94.

413 **SCOTT, G., LAMBE, N. R. and HITCHCOCK, D.** (1997) Ability of laying hens to negotiate  
414 horizontal perches at different heights, separated by different angles. *British Poultry Science* **38**:  
415 48–54.

416 **STRATMANN, A., FROHLICH, E. K. F., GEBHARDT-HENRICH, S., HARLANDER-**  
417 **MATAUSCHEK, A., WÜRBEL, H. and TOSCANO, M. J.** (2015) Modification of aviary  
418 design reduces incidence of falls, collisions and keel bone damage in laying hens. *Applied Animal*  
419 *Behaviour Science* **165**: 112-123.

420 **STRATMANN, A., FROHLICH, E., WÜRBEL, H. and GEBHARDT-HENRICH, S. G.**  
421 (2013) Crashes of laying hens in aviary systems. *Proceedings of the Joint Meeting of the 33rd*  
422 *International Ethological Conference (IEC) & the Association for the Study of Animal Behaviour*  
423 *(ASAB) Conference*, Newcastle-Gateshead, UK.

424 **STRATMANN, A., TOSCANO, M. J., FROHLICH, E. K. F., HARLANDER-**  
425 **MATAUSCHEK, A. and GEBHARDT-HENRICH, S.** Do soft perches reduce keel bone  
426 fractures in laying hens? Accepted to *PlosOne*.

427 **TARLTON, J. F., WILKINS, L. J., TOSCANO, M. J., AVERY, N. C. and KNOTT, L.**  
428 (2013) Reduced bone breakage and increased bone strength in free range laying hens fed omega-  
429 3 polyunsaturated fatty acid supplemented diets. *Bone* **52**: 578–586.

430 **THIRUVENKADAN, A. K., PANNEERSELVAM, S. and PRABAKARAN, R.** (2010) Layer  
431 breeding strategies: an overview. *Worlds Poultry Science Journal* **66**: 477–502.

432 **TIEMEIER, O. W.** (1941) Repaired bone injuries in birds. *Auk* **58**: 350–359.

433 **TILLMANN, J. E.** (2009) Fear of the dark: night-time roosting and anti-predation behaviour in  
434 the grey partridge (*Perdix perdix* L.). *Behaviour* **146**: 999–1023.

435 **TOBALSKE, B. W. and DIAL, K. P.** (2000) Effects of body size on take-off flight performance  
436 in the Phasianidae (Aves). *Journal of Experimental Biology* **203**: 3319–3332.

437 **TOBALSKE, B. W. and DIAL, K. P.** (2007) Aerodynamics of wing-assisted incline running in  
438 birds. *Journal of Experimental Biology* **210**: 1742–1751.

439 **TOBALSKE, B. W., HEDRICK, T. L., DIAL, K. P. and BIEWENER, A. A.**(2003)  
440 Comparative power curves in bird flight. *Nature* **421**: 363–366.

441 **TOMASZEWSKI, P. K., VERDONSCHOT, N., BULSTRA, S. K. and VERKERKE, G. J.**  
442 (2010) A comparative finite-element analysis of bone failure and load transfer of osseointegrated  
443 prostheses fixations. *Annals of Biomedical Engineering* **38**: 2418–2427.

444 **TOSCANO, M. J., BOOTH, F., WILKINS, L. J., AVERY, N. C., BROWN, S. B.,**  
445 **RICHARDS, G. and TARLTON, J. F.** The effects of long (C20/22) and short (C18) chain  
446 omega-3 fatty acids on keel bone fractures, bone biomechanics, behaviour and egg production in  
447 free range laying hens. Accepted to *Poultry Science*

448 **TOSCANO, M. J., BOOTH, F., WILKINS, L. J., BROWN, S. B., RICHARDS, G. and**  
449 **TARLTON, J. F.** (2014) Use of an impact tester to assess the likelihood of fractures occurring  
450 against key bird- and motion-related factors. *Proceedings of the 2014 Poultry Science*  
451 *Association Annual Meeting*, Corpus Christi.

452 **TOSCANO, M. J., WILKINS, L. J., MILBURN, G., THORPE, K. and TARLTON, J. F.**  
453 (2013) Development of an ex vivo protocol to model bone fracture in laying hens resulting from  
454 collisions. (PE Witten, Ed.). *PLoS One* **8**:e66215.

455 **WARREN, D. E.** (1937) Physiological and genetic studies of crooked keels in chickens. Kansas  
456 Agricultural Experiment Station Technical Bulletin:**44**.

457 **WATKINS, B. A., LI, Y., LIPPMAN, H. E. and FENG, S.** (2003) Modulatory effect of  
458 omega-3 polyunsaturated fatty acids on osteoblast function and bone metabolism. *Prostaglandins*  
459 *Leukotrienes Essential Fatty acids* **68**: 387–398.

460 **WHITEHEAD, C. C.** (2004a) Skeletal disorders in laying hens: the problem of osteoporosis and  
461 bone fractures. PERRY, G.C.. (Ed) *Welfare of the Laying Hen*, pp. 259-270 (Wallingford, CABI  
462 Publishing).

463 **WHITEHEAD, C. C.** (2004b) Overview of bone biology in the egg-laying hen. *Poultry Science*  
464 **83**: 193–199.

465 **WHITEHEAD, C. C. and FLEMING, R. H.** (2000) Osteoporosis in cage layers. *Poultry*  
466 *Science* **79**: 1033–1041.

467 **WILKINS, L. J., BROWN, S.N., ZIMMERMAN, P. H., LEEB, C. and NICOL, C. J.** (2004)  
468 Investigation of palpation as a method for determining the prevalence of keel and furculum  
469 damage in laying hens. *Veterinary Record* **155**: 547–549.

470 **WILKINS, L. J., MCKINSTRY, J. L., AVERY, N.C., KNOWLES, T. G., BROWN, S. N.,**  
471 **TARLTON, J and NICOL, C. J.** (2011) Influence of housing system and design on bone  
472 strength and keel bone fractures in laying hens. *Veterinary Record* **169**: 414.